# FOSSIL MAMMALS FROM MONTANA

## Pt. 2.    Rodents from the Early Oligocene Pipestone Springs Local Fauna

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This is the second in a series of papers reviewing materials in the Carnegie Museum collections of vertebrate fossils from Tertiary localities in Montana. I would like to thank C. Lewis Gazin of the United States National Museum, M. C. McKenna of the American Museum of Natural History, and W. D. Turnbull of the Chicago Natural History Museum, for the loan of material in their care. Carnegie Museum field parties were able to make later collections through the generous support of the Childs Frick Corporation. The illustrations are by Mr. Clifford J. Morrow and were made possible by a grant from the Gulf Oil Corporation.

The first collection of fossil vertebrates from the Pipestone Springs locality near Whitehall, Montana, was made by Earl Douglass in 1899; and the first specimens were described by him in 1901. Included in this first paper on the Pipestone Springs fauna were descriptions of three new rodents: *Cylindrodon fontis, Sciurus jeffersoni,* and *Eumys minor.* Matthew (1903) added three new rodent species to the fauna: *Ischyromys veterior, Sciurus (Prosciurus) vetustus,* and *Gymnoptychus minimus,* all collected in 1902 by parties from the American Museum of Natural History. Burke (1935) described a new cylindrodontid, *Pseudocylindrodon neglectus,* from the fauna; and Wood (1937), in his monograph of the White River rodents, included descriptions of all species known from Pipestone Springs and recorded the presence of *Ischyromys pliacus* in the fauna. McGrew (1941) reported the occurrence of *Heliscomys* at Pipestone Springs; and Donohoe (1956), the most recent author to name a rodent from the assemblage, described *Pipestoneomys bisulcatus.*

A review of this rich fauna has not been undertaken since Matthew's

contribution in 1903, and the rodents have not been reviewed since Wood's paper in 1937. In recent years, collecting has been done at Pipestone Springs by a number of institutions. The largest collections are those made by J. LeRoy Kay for Carnegie Museum and by Jean Hough and C. Lewis Gazin for the United States National Museum. That restudy of these collections would contribute significantly to our knowledge is shown by the fact that prior to this report 69 rodent specimens representing 10 species had been described or mentioned in the literature, and of these 41 represented *Ischyromys-Titanotheriomys*. There are now in the Carnegie Museum collections alone 335 specimens of rodents representing all previously described species plus two new genera and one new species of eomyids, bringing the total number of rodent species known from Pipestone Springs to 13. They are:

|  | No. of Specimens CM Coll. |
|---|---|
| Family PARAMYIDAE | |
| *Prosciurus vetustus* Matthew | 8 |
| Family ISCHYROMYIDAE | |
| *Titanotheriomys veterior* (Matthew) ⎱ | 143 |
| *Ischyromys pliacus* Troxell ⎰ | |
| Family CYLINDRODONTIDAE | |
| *Cylindrodon fontis* Douglass | 75 |
| *Pseudocylindrodon neglectus* Burke | 8 |
| Family ?SCIURIDAE | |
| *?Protosciurus jeffersoni* (Douglass) | 3 |
| Family ?CASTORIDAE | |
| *Pipestoneomys bisulcatus* Donohoe | 1 |
| Family EOMYIDAE | |
| *Adjidaumo minimus* (Matthew) | 3 |
| *Paradjidaumo minor* (Douglass) | 86 |
| *Yoderimys burkei*, new species | 1 |
| *Namatomys lloydi*, new genus and species | 2 |
| *Aulolithomys bounites*, new genus and species | 2 |
| Family HETEROMYIDAE | |
| *Heliscomys* cf. *H. vetus* Cope | 3 |

To the best of my knowledge all of the material used for this report was collected from the "Main Pocket" (which lies to the northwest of the old golf course, S.29, T.2N., R.5W., Jefferson Co., Montana) at

Pipestone Springs. No material has been included that is known to have been collected from the Little Pipestone locality south of U.S. Highway 105 or from exposures north of the railroad tracks. Matthew (1903) was the first to recognize that the exposures to the north of the railroad were probably, at least in part, of Orellan age. There is also a possibility that sediments younger than those at the main locality are present in the Little Pipestone area. For this reason only specimens from the classic Pipestone Springs locality have been used and these are believed to be from a single unit fauna of Chadronian age.

Of the seven families of rodents found at Pipestone Springs, six were previously known from the early Oligocene, with only the Sciuridae here being tentatively recorded from the Chadronian for the first time. *Pipestoneomys bisulcatus* was described as an aplodontid by Donohoe (1956), and recently Alf (1962) has suggested castorid affinities for this species. As discussed later, the evidence is equivocal for its inclusion in either family, but to avoid further confusion in the literature it is here retained in the ?Castoridae with the strong possibility that the genus may well prove to belong in neither the Aplodontidae nor the Castoridae. One rodent family known to occur in the early Oligocene, the Eutypomyidae, has not been recognized in the Pipestone Springs fauna. The Eutypomyidae are well represented in certain early Oligocene faunas; but with the exception of a single $P_4$ (Wood, 1937: 233) from Thompson Creek, Montana, members of this family are not known to occur outside the Great Plains area. It is possible, therefore, that at least in the early Oligocene, *Eutypomys* was restricted to the plains and did not live in the intermontane areas.

Three rodent species particularly abundant in the collections are *Titanotheriomys veterior, Cylindrodon fontis,* and *Paradjidaumo minor,* and these evidently lived in the immediate area of deposition. *Ischyromys pliacus, Prosciurus vetustus,* and *Pseudocylindrodon neglectus,* while not as abundantly represented as the above three, are present in numbers which suggest that they lived close to, if not in, the immediate area. *Adjidaumo minimus* and *Heliscomys vetus* are extremely small forms and the paucity of individuals collected to date could reflect a collecting bias rather than actual rareness in the deposit. The remaining five species are medium to large-sized forms and their rare occurrence in the fauna is probably not the result of sampling error but rather may indicate that these animals lived at some distance from the area of deposition.

Konizeski (1961) has suggested a similarity of early Oligocene en-

vironment for the Douglass Creek, Canyon Ferry, and Pipestone Springs basins, with each basin containing a central lake surrounded by marshland which is in turn ringed by upland coniferous forests. In this type of situation more abundant forms were probably lake border species, with the rare species possibly inhabiting the upland forest areas.

The following abbreviations are used throughout: AMNH, American Museum of Natural History; CNHM, Chicago Natural History Museum; CM, Carnegie Museum; USNM, United States National Museum; YPM, Yale Peabody Museum; a-p, anteroposterior; tr. transverse.

All measurements are in millimeters. When two transverse measurements are given, the first is the width across the protoloph or metalophid, and the second is the width of the metaloph or hypolophid.

## SYSTEMATIC REVIEW

### Family PARAMYIDAE Miller and Gidley, 1918
### Genus *Prosciurus* Matthew

### *Prosciurus vetustus* Matthew
### Figure 1

*Sciurus (Prosciurus) vetustus* Matthew, 1903.
*Prosciurus vetustus* Matthew, 1910.

TYPE: AMNH 9626, partial left maxilla with $P^3$-$M^3$.

HYPODIGM: CM 9785, $LP^4$; CM 10111, fragment of left maxilla with $P^3$-$M^1$; CM 10115, fragment of left maxilla with $M^1$-$M^3$. CNHM PM 8615, partial left maxilla and internal wall of orbit and infraorbital foramen with $P^3$-$M^3$. CM 9828, partial right mandible with $P_4$-$M_3$; CM 9870, partial right mandible with $P_4$-$M_3$; CM 10113, partial right mandible with $M_1$-$M_2$; CM 10116, partial right mandible with $P_4$-$M_3$. CNHM PM 8612, partial right mandible with $P_4$-$M_3$. CNHM UM 405, partial right mandible with $dP_4$-$M_2$.

EMENDED DIAGNOSIS: Double metaconules on $P^4$-$M^3$; upper cheek teeth wider than in *Prosciurus relictus;* hypolophids on $P_4$-$M_3$ not as long as in *P. relictus;* width of $M_1$-$M_2$ equals length.

DESCRIPTION: The upper cheek teeth have been described (Matthew, 1903, and Wood, 1937) and only a few details need be added here. The protocone on $P^4$-$M^3$ is constricted anteroposteriorly and rises to a sharp peak. The metaloph on $P^4$-$M^2$ is constricted and fuses with the protocone well down its internal face. Prominent mesostyles are present on $P^4$-$M^3$ and are set off from the paracone and metacone by a narrow valley.

The mandible and lower dentition have not been previously described for this species. In structure and general proportions the mandible

resembles that of *Prosciurus relictus,* with a short diastema, little or no depression of the dorsal surface anterior to $P_4$, and a deep and heavy body under $P_4$-$M_3$. The mental foramen lies about halfway down the side of the mandible midway between $P_4$ and the incisor. The masseteric fossa terminates under the middle of $M_1$, and the dorsal and ventral ridges are strongly developed.
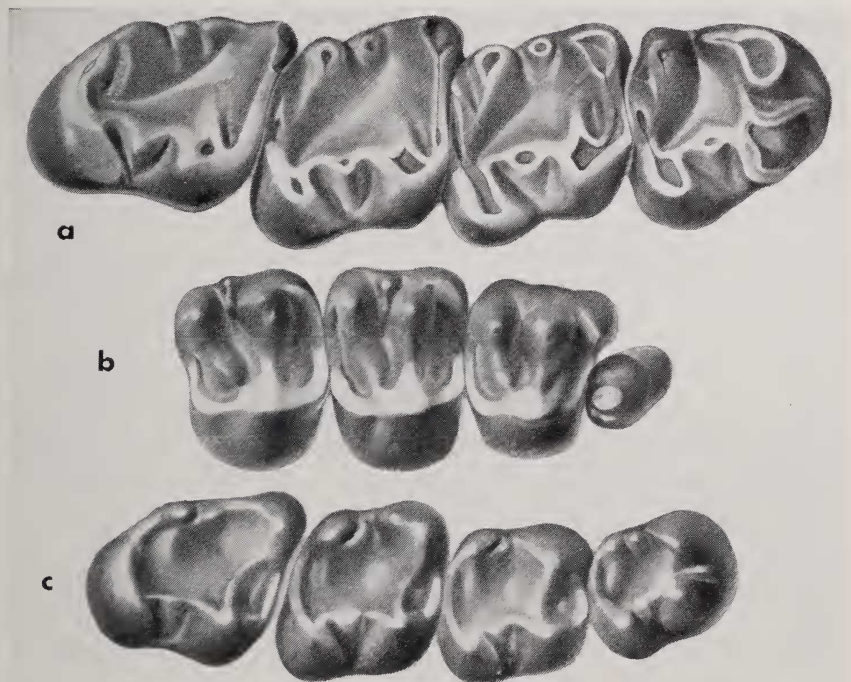


Fig. 1  **a.** *Prosciurus vetustus,* CM 9870, $RP_4$-$M_3$, x13½.  **b-c.** *?Prosciurus jeffersoni,* **b.** CM 10112, $RP^3$-$M^2$, x6½.  **c.** CM 736, Type, $RP_4$-$M_3$, x7.

The anterior half of $P_4$ is partially compressed transversely, but the protoconid and metaconid are completely separated by a distinct trigonid basin. The mesoconid is large, filling most of the buccal valley on $P_4$ and on $M_1$-$M_3$. The mesostylid on $P_4$ is fused into the posterior border of the metaconid; on $M_1$-$M_2$ it is a large and distinct cusp. The hypolophid on $P_4$ is very short and curves into the posterolophid; on $M_1$-$M_2$ it is slightly longer but also merges with the posterolophid. The width of $M_1$ and $M_2$ equals the length, and the teeth are rhomboidal in outline. There is no distinct anterior cingulum on $M_1$-$M_3$; the lophid which

forms the anterior border of the teeth passes directly across the crown from the center of the metaconid to the antero-internal corner of the protoconid. The metaconid on $M_1$-$M_3$ lies at the extreme antero-internal corner of the teeth and does not curve back over the talonid basin. The metalophid is complete on $M_1$ and the trigonid basin is thus closed posteriorly; on $M_2$-$M_3$ the basin is open with the metalophid incomplete. $M_3$ is elongate antero-posteriorly with an expanded hypoconid and posterolophid.

MEASUREMENTS IN MILLIMETERS

|  |  | No. of Specimens | Mean | Observed Range |
|---|---|---|---|---|
| Alveolar length | $P_4$-$M_3$ | 4 | 8.1 | 7.9-8.2 |
| Length of diastema | | 4 | 3.6 | 3.3-4.0 |
| Depth below $M_1$ | | 4 | 5.6 | 4.8-6.0 |
| $P^3$ | a-p | 2 | .75 | .7- .8 |
| | tr. | 2 | .85 | .8- .9 |
| $P^4$ | a-p | 3 | 1.73 | 1.7-1.8 |
| | tr. | 3 | 2.17 | 2.1-2.2 |
| $M^1$ | a-p | 4 | 1.71 | 1.7-1.8 |
| | tr. | 4 | 2.35 | 2.3-2.5 |
| $M^2$ | a-p | 3 | 1.73 | 1.7-1.8 |
| | tr. | 3 | 2.35 | 2.3-2.5 |
| $M^3$ | a-p | 2 | 1.90 | 1.9 |
| | tr. | 2 | 2.10 | 2.0-2.2 |
| $dP_4$ | a-p | 1 | — | 1.54 |
| | tr. | 1 | — | 1.25 |
| | tr. | 1 | — | 1.43 |
| $P_4$ | a-p | 4 | 1.87 | 1.7-2.0 |
| | tr. | 4 | 1.54 | 1.5-1.6 |
| | tr. | 4 | 1.83 | 1.8-1.9 |
| $M_1$ | a-p | 5 | 1.77 | 1.7-1.9 |
| | tr. | 5 | 1.82 | 1.7-1.9 |
| | tr. | 5 | 1.88 | 1.8-2.0 |
| $M_2$ | a-p | 5 | 1.88 | 1.8-2.0 |
| | tr. | 5 | 2.02 | 1.9-2.1 |
| | tr. | 5 | 2.02 | 1.9-2.1 |
| $M_3$ | a-p | 4 | 2.22 | 2.2-2.3 |
| | tr. | 4 | 1.99 | 1.9-2.1 |
| | tr. | 4 | 1.77 | 1.6-1.9 |
| I | a-p | 3 | 2.11 | 2.0-2.1 |
| | tr. | 3 | 1.53 | 1.5-1.6 |

Alveolar length $P^3$-$M^3$ CNHM PM 8615 7.3

AFFINITIES: *Prosciurus vetustus* is the oldest species of the genus that is known from adequate material[1] and could have been ancestral to *P. relictus* of the Orellan, although the presence of double metaconules in the Chadron species might argue against such a derivation. In all other respects, however, the Pipestone Springs species is ideally suited for such an ancestral position. A lengthening of $M_1$-$M_2$ and an increase in the development of the hypolophid on $P_4$-$M_3$ are all that is needed to bring about such a transition. Likewise, *P. vetustus* could be close to the ancestry of *Cedromus wardi*. The short hypolophids are characteristic of both species, those in *Cedromus wardi* being slightly stronger than in *P. vetustus*. The primary difference between the two species lies in the anteroposteriorly elongate $M_1$-$M_2$ and, as in *P. relictus,* in the presence of only single metaconules on $P^4$-$M^3$ in *Cedromus.*

The ancestry of *Prosciurus vetustus* is unknown. Wood (1962: 226) included the late Eocene *Mytonomys* in the subfamily Prosciurinae but stated that *Mytonomys* was certainly not ancestral to *Prosciurus* or to any other known member of the subfamily.

## Family ISCHYROMYIDAE Alston, 1876

The ischyromyids *Titanotheriomys veterior* and *Ischyromys pliacus* are treated only briefly in this review. Both have been previously reported from this fauna, and in the Carnegie Museum collections there are 143 specimens representing these two species. In the course of this study, however, it became apparent that it is next to impossible to assign most of the material with any degree of confidence, even when dealing with complete dentitions, to one genus or the other as they are presently understood. After examining other material assigned to *Ischyromys typus* and *I. pliacus,* both Orellan forms, and also specimens of *Titanotheriomys wyomingensis* from Beaver Divide, Wyoming, several other problems regarding ischyromyid systematics have come to light. These problems can only be resolved by a thorough review of all the Oligocene ischyromyid material. For these reasons, while both species are listed below, no attempt has been made to add to the information supplied by Wood (1937: 188-191, 193-197). No formal diagnoses have ever been given for either *Ischyromys pliacus* or *Titanotheriomys veterior* and none are attempted here.

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[1] *P. saskatchewaensis* and *P.* aff. *lohiculus,* both from Cypress Hills (Wood, 1937), are each known from only a single tooth and hence can offer little information for phylogenetic interpretation.

Genus *Ischyromys* Leidy

*Ischyromys pliacus* Troxell

*Ischyromys pliacus* Troxell, 1922.

TYPE: YPM 12511, right mandible with $P_4$-$M_3$.

Genus *Titanotheriomys* Matthew

*Titanotheriomys veterior* (Matthew)

*Ischyromys veterior* Matthew, 1903.
*Ischyromys* (*Titanotheriomys*) *veterior* Matthew, 1910.
*Titanotheriomys veterior* (Matthew), Miller and Gidley, 1920.

LECTOTYPE: AMNH 9658, left mandible with $P_4$-$M_3$.

Family CYLINDRODONTIDAE Miller and Gidley, 1918
Genus *Pseudocylindrodon* Burke

*Pseudocylindrodon neglectus*
Figure 2

*Cylindrodon fontis* Matthew, 1903, in part.
*Pseudocylindrodon neglectus* Burke, 1935.

TYPE: USNM 13758, partial left mandible with $P_4$-$M_3$.

HYPODIGM: CM 10100, incomplete skull. USNM 13757, left mandible with $P_4$-$M_3$; USNM 13759, right mandible with $P_4$-$M_1$. AMNH 9644, left mandible with $dP_4$-$M_2$; AMNH 9646, partial right mandible with $P_4$. CM 9325, right mandible with $M_2$-$M_3$; CM 10007, right mandible with $P_4$-$M_3$; CM 10011, right mandible with $P_4$-$M_3$; CM 10027, left mandible with $P_4$-$M_3$; CM 10042, $RM_2$-$M_3$; CM 10091, right mandible with $M_1$-$M_3$; and CM 10096, left mandible with $P_4$-$M_3$, all mandibles incomplete.

EMENDED DIAGNOSIS: Near size of *Pseudocylindrodon medius*, cheek teeth higher crowned; anterior cingulum on $P^4$ short, fused with antero-internal face of paracone; mesostyle present on $P^4$-$M^2$; no hypolophid crest on $P_4$; mesostylid fused to posterior metaconid slope on $P_4$-$M_3$; central and posterior basins closed internally on $M_1$-$M_3$; hypoconid, hypolophid and posterior cingulum reduced on $M_3$.

DESCRIPTION: The skull fragment agrees in most respects with the corresponding parts of *Pseudocylindrodon medius*, differing only in a few details. *P. neglectus* differs from *P. medius* in the greater expansion of the premaxilla at the premaxillary-frontal contact with the result that the dorsal expansion of the maxilla is reduced. The lacrimal may

have been somewhat larger in *P. neglectus* but its exact extent is impossible to determine due to breakage. The sphenopalatine foramen is not as elongate antero-posteriorly and is directed more vertically in *P. neglectus* than in *P. medius.* The posterior narial opening is narrow, more as in *Cylindrodon* than in *P. medius,* and is carried farther forward than in the latter species. In size and general proportions *P. neglectus* is nearly identical with *P. medius.*

The mandible is short, deep, and rather heavy, with a short diastema. In general it is very similar to that of *P. medius* but is deeper below the cheek teeth. Two mental foramina are present, one lying below the anterior root and the other below the posterior root of $P_4$. The masseteric fossa extends forward to below the anterior end of $M_2$. Neither the dorsal nor ventral masseteric ridges are prominent, and the fossa is not constricted anteriorly but terminates in a broad curve.

The upper incisors have a greater antero-posterior than transverse diameter and are ovate in cross section. The anterior face is rounded and the enamel is limited to the anterior surface. The pulp cavity is angulate.

The upper dentition of *P. neglectus* has not previously been known. The skull fragment, CM 10100, has the complete dentition, with the exception of $RP^3$, preserved in a moderately worn condition. In *P. neglectus* $P^3$ is a more slender tooth than it is in *P. medius* but in both species it is a simple peg with no trace of accessory cusps or cingula such as are seen in *Ardynomys.* The fourth upper premolar and $M^1$-$M^2$ are of nearly equal size and are broadly triangular, while $M^3$ is much smaller and oval in occlusal view. As in *Cylindrodon* and *Ardynomys* $P^4$-$M^3$ are unilaterally hypsodont. Wear has obliterated any trace of the reduced hypocone, the condition described by Burke (1938: 268) for *P. medius.*

On $P^4$ the anterior cingulum is extremely short and fails to open on the buccal margin of the tooth but bends back into the base of the paracone. A small shallow pit is thus formed between the anterior cingulum and the protoloph. In *P. medius* the anterior cingulum is much longer and reaches the buccal margin of $P^4$, with the basin between the cingulum and protoloph opening buccally. The protoloph and metaloph are complete on $P^4$. There is no protoconule but the metaconule is large and fuses with the posterior cingulum. Two small pits are thus formed between the posterior cingulum and metaloph. The central basin opens to the buccal margin but this opening is partially constricted by a prominent mesostyle situated at the base of the paracone.

The first and second upper molars are essentially identical in structure. The anterior cingulum reaches the buccal border and the anterior basin is open. The central basin is only partially closed by a large mesostyle in both teeth. The connection of the metaconule and posterior cingulum can be seen on $M^2$, but wear has obliterated any traces of this crest on $M^1$. The posterior cingulum is short and meets the posterior side of the metacone internal to the buccal margin of the tooth.

The third molar is considerably smaller than $M^1$-$M^2$, due partially to its unworn condition but also to a reduction in the size of the protocone, metaloph, metaconule and posterior cingulum. The latter elements are greatly compressed with metaconule-metacone appearing almost as a single cusp. A small pit is cut off between the metaloph, metaconule and posterior cingulum but the buccal end of the posterior cingulum does not fuse with the metacone as it does on $M^1$-$M^2$. The anterior cingulum reaches to the buccal side of $M^3$ as it does in $M^1$-$M^2$. No mesostyle is present on $M^3$.

The lower incisor is oval in cross section, with a rounded anterior face. The posterior border is more constricted than in the upper incisor but the two agree fairly closely in outline. The enamel is for the most part confined to the anterior face, overlapping only slightly onto the lateral margins of the tooth. The pulp cavity is long and narrow.

In AMNH 9644 the anterior half of the crown of $dP_4$ is broken, but enough of the tooth is preserved to show the presence of a well developed hypolophid passing from the entoconid to the antero-internal corner of the hypoconid. This crest is absent in the permanent premolar of *P. neglectus* but is well developed in $P_4$ of *P. medius*.

The lower cheek teeth are higher crowned than are those of *P. medius* but agree closely with that species in size and general shape. The anterior half of $P_4$ is narrow, with the protoconid and metaconid closely appressed and separated by only a shallow groove on the anterior face of the tooth. The mesostylid is fused into the posterior slope of the metaconid, as it is on $M_1$-$M_3$, forming a crest which sweeps back to join the entoconid and thus completely cuts off the central basin. In *P. medius* the mesostylid is absent and the central valley opens on the lingual

Fig. 2  *Pseudocylindrodon neglectus.* **a.** CM 10100, $LP^3$-$M^3$, x10. **b.** CM 10091, right mandible, x5. **c.** AMNH 9644, $LdP_4$-$M_2$, Type, x10. **d.** CM 10096, $LP_4$-$M_3$, x10, **e.** CM 10007, $RP_4$-$M_3$, x10.
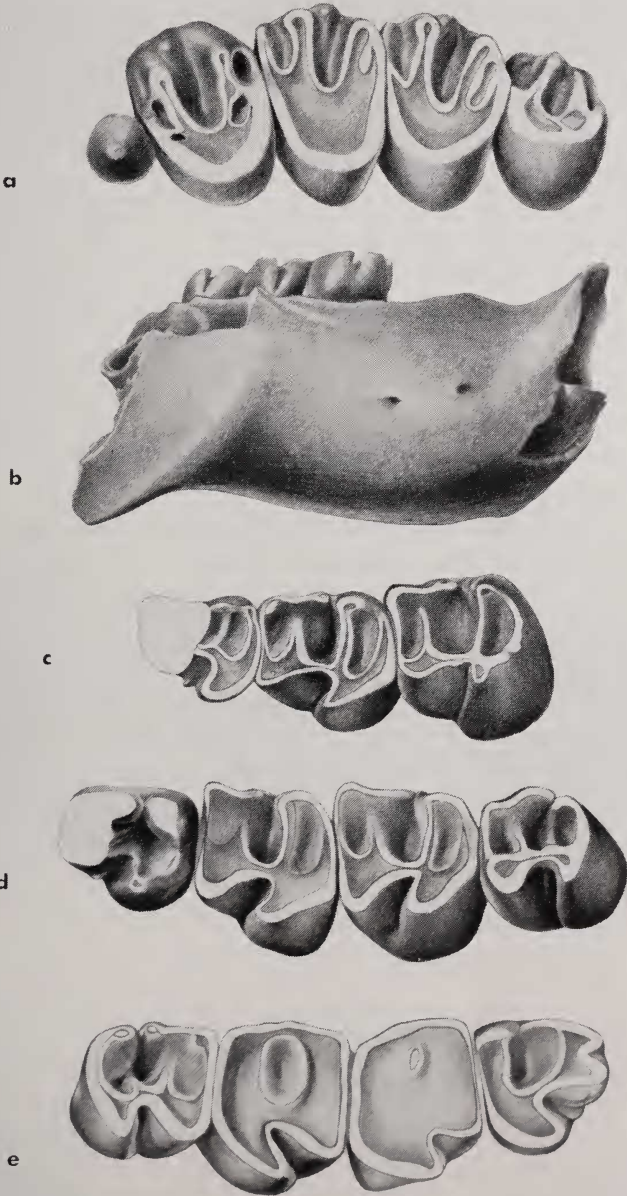
margin of $P_4$-$M_3$. The hypoconid on $P_4$ is strongly developed but there does not appear to be any hypoconulid.

The lower molars are similar in structure, although $M_3$ is much smaller than $M_1$-$M_2$ and has a reduced hypocone, hypolophid, and posterior cingulum. In all three teeth the metalophid is well developed and with the anterior cingulum isolates a very shallow trigonid pit between the protoconid and metaconid. The central basin is deep but is obliterated at advanced wear stages; the anterior and posterior basins disappear at a much earlier wear stage. The hypolophid on $M_1$-$M_2$ is strongly developed but is weak to absent on $M_3$. The hypoconulid is not distinct as a separate cusp on $M_1$-$M_2$ but the buccal end of the posterior cingulum where it meets the hypoconid is enlarged. The cingulum passes from this area across and up to fuse with the entoconid near the top of the cusp. On $M_3$ the hypoconid and posterior cingulum are reduced in size and there is no enlargement of the buccal end of the posterior cingulum.

AFFINITIES: *Pseudocylindrodon neglectus,* while sharing some features such as mesodont cheek teeth and double mental foramina with *P. medius* from the early Oligocene of McCarty's Mountain, differs from that species in the possession of mesostyles and stylids, the absence of a hypolophid crest on $P_4$, and the almost complete closure internally of the transverse valleys on $P_4$-$M_3$. Neither species of *Pseudocylindrodon* could be directly ancestral to *Cylindrodon fontis,* their contemporary, but *P. medius* seems to be closer to *Cylindrodon* than is *P. neglectus.* The absence of mesostyles on $P^4$-$M^3$ and the presence of a hypolophid on $P_4$ would tend to support this conclusion. *P. neglectus,* so far as is now known, left no descendants.

MEASUREMENTS IN MILLIMETERS

CM 10100

| | | | | | |
|---|---|---|---|---|---|
| Alveolar length $P^3$-$M^3$ | | 7.0 | $M^2$ | a-p | 1.7 |
| $P^3$ | a-p | .7 | | tr. | 2.4 |
| | tr. | 1.0 | $M^3$ | a-p | 1.4 |
| $P^4$ | a-p | 1.6 | | tr. | 1.9 |
| | tr. | 2.5 | $I^1$ | a-p | 1.9 |
| $M^1$ | a-p | 1.7 | | tr. | 1.8 |
| | tr. | 2.5 | | | |

| | AMNH 9325 | CM 10007 | CM 10011 | CM 10027 | CM 10091 | CM 10096 |
|---|---|---|---|---|---|---|
| Alveolar length $P_4$-$M_3$ | 7.6 | 7.2 | 7.2 | 7.3 | 7.5 | 7.3 |
| Length of diastema | 3.1 | 3.4 | — | 3.5 | 3.3 | 3.2 |
| Length below $M_1$ | — | 5.8 | 5.5 | 5.7 | 5.4 | 5.3 |
| $P_4$   a-p | — | 1.6 | — | — | — | — |
|     tr. | — | 1.8 | 1.8 | — | — | — |
| $M_1$   a-p | — | 1.6 | 1.6 | — | 1.7 | 1.7 |
|     tr. | — | 2.2 | 2.1 | — | 2.1 | 2.1 |
| $M_2$   a-p | 1.8 | 1.7 | 1.7 | — | 1.8 | 1.8 |
|     tr. | 2.1 | 2.1 | 2.1 | — | 2.1 | 2.1 |
| $M_3$   a-p | 1.6 | 1.7 | 1.6 | — | 1.6 | 1.6 |
|     tr. | 1.8 | 1.7 | — | — | 1.7 | 1.8 |
| $I_1$   a-p | 2.1 | — | — | 2.0 | — | — |
|     tr. | 1.9 | — | — | 1.7 | — | — |

## Genus *Cylindrodon* Douglass

### *Cylindrodon fontis* Douglass
#### Figure 3

*Cylindrodon fontis* Douglass, 1901

LECTOTYPE: CM 738a, partial left mandible with $M_1$-$M_3$. Douglass (1901: 251) did not designate a type but mentioned two specimens, Nos. 38 and 39, and figured No. 38. These numbers referred to his own personal collection. When the specimens were turned over to Carnegie Museum they were re-numbered 738 and 738a. Wood (1937: 202) designated 38 (CM 738) as the type. This specimen has since been lost. Therefore CM 738a, Douglass' second syntype (39), is here designated the lectotype.

REFERRED SPECIMENS: 75 specimens in the Carnegie Museum collections and numerous specimens in the AMNH, CNHM, and USNM collections.

EMENDED DIAGNOSIS: Cheek teeth hypsodont; $dP^3$ present but $P^4$ displaces $dP^3$-$dP^4$, leaving only four teeth in permanent dentition; anterior and posterior basins of $dP^4$, $M^1$-$M^2$ completely enclosed, and central basins open buccally only during earliest wear stages; no anterior basin on $P^4$ and anterior cingulum absent; posterior basin of $P^4$ enclosed and divided by short ridge from metaloph to posterior cingulum; $M^1$-$M^3$ much longer than wide when unworn, becoming wider than long with wear; $dP_4$ narrow, elongate, with strong hypolophid and discrete anterior cingulum; $P_4$ shorter, more robust, without anterior cingulum; anterior and posterior basins enclosed on $M_1$-$M_2$; $M_1$-$M_3$ longer than wide when unworn, becoming nearly cylindrical with wear.

DESCRIPTION: Known parts of the skull of *Cylindrodon fontis* agree well with those of *Pseudocylindrodon*. The rostrum is short and broad. The nasal-frontal and premaxillary-frontal sutures lie slightly farther

behind the anterior end of the orbit in *C. fontis* than they do in *Pseudocylindrodon,* and the premaxillary-frontal contact is rather broad. The infra-orbital foramen lies higher on the face than it does in *Pseudocylindrodon,* and the ventral surface of the zygoma is broader and more deeply excavated in *C. fontis.* The posterior palatine notch lies opposite the middle of $M^2$.

The mandible is short and heavy, having a very short diastema. The single mental foramen is anterior to $P_4$ and just below the alveolar level. The masseteric fossa is delimited by strong dorsal and still stronger ventral masseteric ridges which meet below the anterior edge of $M_2$. The ascending ramus rises rather steeply from a point opposite the anterior end of $M_2$, but in none of the available material from Pipestone Springs is more than the root of the ascending ramus preserved.

The upper incisors are oval in cross section with the enamel limited to the rounded anterior faces. The pulp cavity is short and narrow.

Both upper and lower cheek teeth are hypsodont. The unilateral hypsodonty seen in *Pseudocylindrodon* is only slightly developed in *Cylindrodon,* where there is almost no difference in crown height between the buccal and lingual margins of the upper teeth and only a slight difference in the lower dentition. When unworn and through the early wear stages the crowns of $M^1$-$M^3$ and $M_1$-$M_3$ are considerably longer than they are wide. In the upper molars the antero-posterior dimension decreases with wear while the transverse dimension increases until the teeth are wider than long. Coinciding with these changes in the upper molars, the occlusal outline of the lower molars changes from rectangular to cylindrical.

In the upper dentition $dP^3$ is present as pointed out by Wood (1937: 201), but it is shed along with $dP^4$ with the eruption of the permanent premolar. The deciduous $P^3$ is a small, very simple peg-like tooth with only a single conical cusp and no trace of cingula. The deciduous $P^4$ resembles $M^1$-$M^2$ in most respects, differing primarily in possessing a more compressed posterior cingulum.

When unworn the occlusal outline of the permanent premolar is nearly square. There is a wide lingual border which shows no distinct cusps, a short metaloph with distinct metaconule, and a narrow posterior cingulum that joins the metacone below the level of the metaloph. Anteriorly, the paracone and lingual shelf are separated by a narrow trench. The paracone is bulbous and there is no indication of a distinct protoloph. With wear the paracone and internal shelf are joined, but the narrow valley between the two cusps remains as a trench for a considerable

distance down the anterior face of the tooth. Posteriorly, there are generally two small ridges running from the metaconule to the posteroloph. In advanced wear stages the premolar takes on the rectangular occlusal outline of $M^1$-$M^2$.

Unworn $M^1$-$M^2$ display four transverse lophs which enclose three basins. The anterior and posterior basins are not as deep as the central basin and are completely enclosed even in unworn teeth. The central basin is open at the buccal margin during early wear stages but is closed by the time $dP^3$-$dP^4$ are shed. The internal borders of $M^1$-$M^2$ are quite long in young individuals but neither the protocone nor hypocone can be distinguished as discrete cusps. The crowns taper toward the base of the molars with a reduction in the width of the anterior and posterior cingula and the anterior and posterior basins. This tapering, coupled with the migration of the wear surface internally, results in the extreme change in occlusal dimensions of $M^1$-$M^2$ and to a lesser degree of $P^4$ and $M^3$. The last element of the crown pattern to be lost on all teeth is the enamel fossette of the central basin. These changes in shape and pattern are shown in figure 3, as is a vertical section of $M^1$ showing the construction and depth of the central basin.

The third upper molar, smallest of the upper cheek teeth, shows a considerable reduction of the posterior half of the crown. The anterior cingulum, protoloph, and metaloph resemble those in $M^1$-$M^2$ but are much shorter. At early stages of wear the posterior basin is open to the rear of the tooth and the well developed posteroloph seen on $M^1$-$M^2$ is absent, as is the expanded postero-internal corner of the crown. With wear the posterior basin is closed by a loph which swings in an arc from the protocone to the rear of the metacone.

The lower incisors are triangular in cross section, with the enamel limited to the rounded anterior face. The pulp cavity is narrow and short.

The deciduous lower premolar is long and slender and is wider posteriorly than anteriorly. A narrow fissure separates the protoconid and metaconid partway down the crown, but with moderate wear these two cusps become fused. The hypolophid consists of only a small, short spur which passes from the hypoconid across to the base of the entoconid. The posterolophid and entoconid are set off at early wear stages by a shallow cleft but with greater wear are fused into a continuous posterolophid.

The permanent lower premolar is shorter and broader than $dP_4$. The protoconid and metaconid, even when $P_4$ is essentially unworn, are
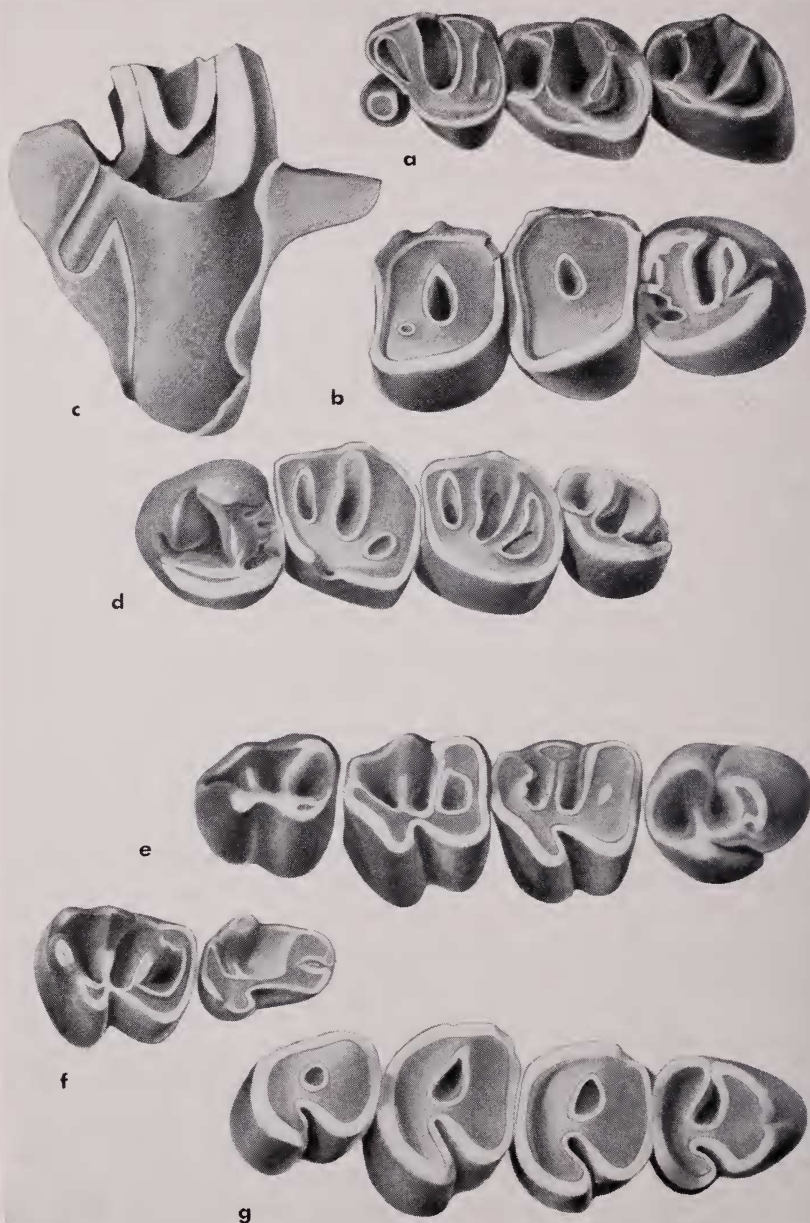
fused into a single anterior column, with the trigonid basin indicated by a very shallow, ephemeral pit. The central basin is deep and almost completely enclosed, with only a shallow slit between the metaconid and entoconid. The hypolophid rises to the occlusal surface and is strongly developed. The posterior cingulum curves from the hypoconid to the entoconid and, with the hypolophid, cuts off a deep posterior basin.

At early stages of wear $M_1$-$M_2$ are longer than wide due to the angular expansion of the hypoconulids and posterior cingula at the crown surface. The posterior cingula terminate well behind the entoconids, where they are met by buttresses from the posterior edge of the entoconids which close off the posterior basins. With wear the posterior borders of $M_1$-$M_2$ become rounded, with the posterior cingula swinging in an arc to the posterior corners of the entoconids and the occlusal outlines taking on a circular appearance. Anteriorly, there is a small trigonid basin cut off by the anterior cingulum and metalophid. This is the shallowest of the three basins and disappears early in the life of the tooth. The central basin is narrow but deep. Along the lingual borders of $M_1$-$M_2$ the metaconid and entoconid are fused into a continuous ridge after little wear, although at the earliest wear stages they are separated by a very narrow trench.

The third lower molar is the smallest of the cheek teeth and here, as in $M^3$, the reduction has been primarily in the posterior elements of the crown. The trigonid resembles that of $M_1$-$M_2$, but, in the talonid, the hypolophid is very short as is the posterior cingulum. The shallow posterior basin is lost rapidly with wear.

AFFINITIES: Only two species of *Cylindrodon* are known, *Cylindrodon fontis* and *C. nebraskensis* Hough and Alf from the Chadron of northwestern Nebraska. The latter species was based on one jaw with badly worn dentition. From the description (Hough and Alf, 1956) this species can not be distinguished from *C. fontis,* and I believe that it may be synonymous with *C. fontis.* However, I have refrained here from synonymyzing it with *C. fontis* as the Nebraska fauna is now under study by A. E. Wood, who has more material from this cylindrodont population.

Wood (1937: 203, figs. 29 and 30) figured and briefly described some

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Fig. 3   *Cylindrodon fontis.* **a.** CM 8904, $LdP^3$-$M^2$, x10. **b.** CM 9223, $RP^4$-$M^2$, x10. **c.** CM 10106, longitudinal section of $LM^1$ showing depth of central fossette, x10. **d.** CM 10030, $LP^4$-$M^3$, x10. **e.** CM 10009, $RP_4$-$M_3$, x10. **f.** CM 10104, $RdP_4$-$M_1$, x10. **g.** CM 10012, $RP_4$-$M_3$, x10.

specimens from Beaver Divide, Wyoming, which he listed as *Cylindrodon,* new species. Examination of these specimens, one of which shows $dP^3$-$dP^4$ and another $dP_4$, along with one or more unworn molars, leads me to consider them a population of *C. fontis.* The characters which are listed as differing from those of *C. fontis,* such as position of mental foramen, narrow $M_3$ talonid, molariform $dP_4$, and straight metalophid, are all duplicated in the Pipestone Springs population.

*Cylindrodon fontis* was evidently an end line of the Cylindrodontidae in North America. It was a widespread species in the early Oligocene, being known from Nebraska, Montana, and Saskatchewan and several localities in Wyoming. No specimens have been reported from later horizons.

MEASUREMENTS IN MILLIMETERS

|  |  | Number of Specimens | Mean | Standard Deviation | Coefficient of Variation | Observed Range |
|---|---|---|---|---|---|---|
| Alveolar length $P^4$-$M^3$ |  | 6 | 7.1 | — | — | 6.5-7.5 |
| Alveolar length $P_4$-$M_3$ |  | 22 | 7.7 | .31 | 4.03 | 7.2-8.5 |
| Length of diastema |  | 16 | 3.4 | .30 | 8.82 | 3.0-4.0 |
| Depth below $M_1$ |  | 21 | 6.1 | .29 | 4.75 | 5.7-6.6 |
| $dP^3$ | a-p | 2 | .75 | — | — | .7- .8 |
|  | tr. | 2 | .85 | — | — | .8- .9 |
| $dP^4$ | a-p | 3 | 1.77 | — | — | 1.7-1.8 |
|  | tr. | 3 | 1.70 | — | — | 1.5-1.8 |
| $P^4$ | a-p | 6 | 1.73 | — | — | 1.6-2.0 |
|  | tr. | 6 | 2.03 | — | — | 1.6-2.7 |
| $M^1$ | a-p | 9 | 1.86 | — | — | 1.5-2.1 |
|  | tr. | 9 | 1.99 | — | — | 1.5-2.7 |
| $M^2$ | a-p | 9 | 1.78 | — | — | 1.5-2.0 |
|  | tr. | 9 | 1.78 | — | — | 1.3-2.4 |
| $M^3$ | a-p | 5 | 1.56 | — | — | 1.4-1.7 |
|  | tr. | 5 | 1.46 | — | — | 1.2-1.7 |
| $I^1$ | a-p | 2 | 1.75 | — | — | 1.5-2.0 |
|  | tr. | 2 | 1.80 | — | — | 1.5-2.1 |
| $dP_4$ | a-p | 4 | 1.87 | — | — | 1.7-2.0 |
|  | tr. | 4 | 1.53 | — | — | 1.4-1.7 |
| $P_4$ | a-p | 21 | 1.77 | .010 | 5.65 | — |
|  | tr. | 21 | 1.71 | .048 | 8.65 | — |

| | | Number of Specimens | Mean | Standard Deviation | Coefficient of Variation | Observed Range |
|---|---|---|---|---|---|---|
| $M_1$ | a-p | 24 | 1.87 | .125 | 6.68 | 1.6-2.2 |
| | tr. | 24 | 1.97 | .150 | 7.61 | 1.6-2.3 |
| $M_2$ | a-p | 24 | 1.82 | .108 | 5.93 | 1.6-2.0 |
| | tr. | 24 | 1.95 | .150 | 7.69 | 1.6-2.2 |
| $M_3$ | a-p | 22 | 1.64 | .086 | 5.24 | 1.4-1.8 |
| | tr. | 22 | 1.45 | .142 | 9.79 | 1.1-1.6 |
| $I_1$ | a-p | 12 | 2.03 | — | — | 1.8-2.2 |
| | tr. | 12 | 1.87 | — | — | 1.8-2.0 |

Family ?SCIURIDAE Gray, 1821
Genus *Protosciurus* Black

*?Protosciurus jeffersoni* (Douglass)
Figure 2

*Sciurus jeffersoni* Douglass, 1901.
*Prosciurus jeffersoni* (Douglass), Matthew, 1909.
? *Prosciurus jeffersoni* (Douglass), Wood, 1937.
*Cedromus jeffersoni* (Douglass), Wood, 1962.

TYPE:   CM 736, partial right mandible with $P_4$-$M_3$.

HYPODIGM:   Type and CM 9329, partial right mandible with $P_4$-$M_3$; CM 10112, fragment of right maxilla with $P^3$-$M^2$. CNHM UM 406, partial left mandible with $P_4$-$M_1$.

EMENDED DIAGNOSIS:   Masseteric fossa terminating under hypoconid of $M_1$ with small muscle scar immediately anterior to fossa; $P^4$-$M^2$ with low lophs and little or no indication of conules; protocone slightly anterior in position, with strong internal protocone-posterior cingulum connection; $M_1$-$M_2$ wider than long; entoconid corners of $M_1$-$M_2$ slightly rounded; trigonid basins on $M_1$-$M_3$ enclosed; no separation between entoconid and posterolophid on $P_4$-$M_2$ but entoconids rise above level of posterolophid; short hypolophid from entoconids into talonid basins of $P_4$-$M_3$; mesostylids small on $P_4$-$M_2$, slightly larger on $M_3$.

DESCRIPTION:   There is no proof for association of the mandible of *?P. jeffersoni* and the upper dentition here referred to the species. The two are of the same size and occlude well, however; and there is no other rodent known in the fauna to which the maxillary fragment could be assigned. Also, since both the upper and lower teeth show a number of resemblances to sciurid dentitions, I believe association of the two is likely.

The third upper premolar is a round, stout peg lying just internal to

the expanded anterior cingulum and parastyle of $P^4$. A small lingual shelf is developed part way down the slope of the single cusp on $P^3$, but the shelf is not carried onto the anterior face of the tooth. $P^4$-$M^2$ are massive teeth with large protocones and low lophs. Expansion of the buccal portion of the anterior cingulum on $P^4$ gives the occlusal surface of the tooth a triangular outline. On $M^1$-$M^2$ the width of the cingulum remains constant, giving the teeth a rectangular occlusal outline. The posterior cingula on $P^4$-$M^2$ are narrow and do not reach the buccal margins of the teeth. Lingually, however, the cingula are broad where they bend anteriorly to join the protocones. This condition is pronounced in $M^1$-$M^2$, not as well developed on $P^4$. The protoloph and metaloph on $P^4$-$M^2$ are low and are fused to the buccal slope of the protocone. Neither protoconules nor metaconules can be distinguished with any certainty within the lophs; but the metalophs, particularly on $M^1$-$M^2$, are partially constricted at the protocone. There is a small mesostyle between the paracone and metacone on $M^1$-$M^2$, but there is no mesostyle on $P^4$.

The mandible is heavy with a short diastema and shallow depression between $I_1$ and $P_4$. The mental foramen lies slightly anterior to $P_4$ and considerably below the dorsal surface of the mandible. The masseteric fossa extends forward to below the hypoconid of $M_1$; anterior to this point a shallow scar extends forward to below the middle of $M_1$. The deeply concave masseteric fossa has a strong dorsal ridge and a gently curved anterior border.

$P_4$-$M_2$ are of approximately equal length, but the premolar is considerably narrower, especially across the trigonid. The trigonid basin on $P_4$ is reduced to a narrow, anteroposteriorly directed slit which is open at both ends. A small elongate anteroconid passes from the protoconid forward to the anterior margin of the tooth. The large trigonid basins on $M_1$-$M_3$ are completely enclosed. The anterior cingulum is thick and on $M_1$ is so swollen as to appear cusp-like. The metalophid is complete on all molars. The apex of the metaconid on $P_4$-$M_3$ is directed buccally and overhangs the trigonid basin. This cusp is also elongate, with its postero-lingual margin drawn out into a buttress which is separated from the entoconid by a narrow valley partially filled by a small mesostylid. The entoconid on $P_4$-$M_3$ rises above the level of the posterolophid but is completely incorporated within the lophid. The posterior borders of $P_4$-$M_2$ curve slightly from the entoconid to the hypoconid. On $M_3$ the posterolophid is expanded posteriorly, making the tooth much longer than $P_4$-$M_2$ and the posterolophid

much heavier than in the anterior teeth. There is a short hypolophid on all the cheek teeth which is directed toward the hypoconid but which fades into the talonid basin about one-third of the distance across the crown. The ectolophid is low and dominated by a small but distinct mesoconid. The buccal valley is wide and deep with the ectolophid set well in from the buccal margin.

The incisor is large but compressed transversely as in sciurids. The enamel is finely wrinkled and covers the anterior and one-quarter of the lateral face. The pulp cavity is slit-like.

MEASUREMENTS IN MILLIMETERS

|  |  | CM 10112 | CM 736 | CM 9329 | CNHM UM 406 |
|---|---|---|---|---|---|
| Alveolar length | $P_4$-$M_3$ | — | 12.7 | 13.2 | — |
| $P^3$ | a-p | 1.1 | — | — | — |
|  | tr. | 1.5 | — | — | — |
| $P^4$ | a-p | 2.7 | — | — | — |
|  | tr. | 3.6 | — | — | — |
| $M^1$ | a-p | 2.9 | — | — | — |
|  | tr. | 3.9 | — | — | — |
| $M^2$ | a-p | 2.9 | — | — | — |
|  | tr. | 3.8 | — | — | — |
| $P_4$ | a-p | — | 2.7 | 2.7 | 2.7 |
|  | tr. | — | 2.4-2.7 | 2.3-2.6 | 2.2-2.6 |
| $M_1$ | a-p | — | 2.7 | 2.9 | 2.7 |
|  | tr. | — | 2.9-3.1 | 3.0-3.1 | 2.6-2.8 |
| $M_2$ | a-p | — | 2.8 | 3.1 | — |
|  | tr. | — | 3.2-3.2 | 3.4-3.3 | — |
| $M_3$ | a-p | — | 3.6 | 3.8 | — |
|  | tr. | — | 3.3-3.0 | 3.6-3.1 | — |
| $I_1$ | a-p | — | — | — | 3.5 |
|  | tr. | — | — | — | 2.0 |

AFFINITIES: *?Protosciurus jeffersoni* has had a checkered taxonomic history, having been referred to three different genera since its description by Douglass (1901). Its most recent reference previous to this study was to *Cedromus* (Wood, 1962).

Before discussing the relationships of *?P. jeffersoni* it should be point-

ed out that there is some question as to whether the skull referred to ?*Cedromus* sp., in which the only upper dentition known for the genus is preserved, is actually referable to that genus (Galbreath, 1953: 59, and Wood, 1962: 233). Galbreath thought the association likely, however, and I agree. I also believe that the skull is probably that of *Cedromus wardi* on the basis of occlusal relationships. As stated earlier, there is no definite basis for assuming the upper dentition here referred to ?*P. jeffersoni* is associated with the type mandible; however, all available evidence suggests such an association and I believe the maxilla is that of ?*P. jeffersoni*.

If these associations prove to be correct, the dentition of ?*Protosciurus jeffersoni* differs from that of *Cedromus wardi* in the following respects: (1) rectangular occlusal outline of $M^1$-$M^2$ effected by the anteroposterior expansion of the protocone and the broad connection of the posterior cingulum and protocone; (2) low lophs on $P^4$-$M^2$; (3) absence of protoconules and metaconules on $P^4$-$M^3$; (4) greater transverse than anteroposterior dimensions of $M_1$-$M_2$; (5) strong anterior cingulum on $M_1$-$M_3$; (6) entoconid partially incorporated in posterolophid on $P_4$-$M_3$; (7) buccal valleys of $P_4$-$M_3$ not filled by mesoconid and ectostylid; (8) posterolophid of $M_3$ greatly expanded.

In characters (1), (5), and (8) ?*Protosciurus jeffersoni* differs from *Cedromus wardi*. The difference between the two species in characters (6) and (7) are ones of degree and here ?*P. jeffersoni* more closely resembles the sciurids than it does *Cedromus*. This suite of characters also distinguishes ?*Protosciurus jeffersoni* from *Prosciurus vetustus, P. relictus* and *Pelycomys*. The only real point of similarity between ?*Protosciurus jeffersoni* and the prosciurines *Cedromus, Prosciurus,* and *Pelycomys* lies in the presence of a hypolophid on $P_4$-$M_3$ in the Pipestone Springs species and in all prosciurines. In ?*Protosciurus jeffersoni* this is a very small structure; in *Cedromus wardi* and *Prosciurus vetustus* it is stronger; and in *Prosciurus relictus* and *Pelycomys* it is still more strongly developed. Although a hypolophid is not known to occur in any sciurid before the late Miocene (Black, 1963b), it is possible that it was present in the early history of the family. The dental similarities between ?*Protosciurus jeffersoni* and *Protosciurus mengi* from the Orellan of Nebraska, and the distinct differences between ?*Protosciurus* Springs species as provisionally referable to the Sciuridae. If ?*Proto-jeffersoni* and the prosciurines, have led me to consider the Pipestone *sciurus jeffersoni* proves to be a sciurid it represents the oldest record for the family.

## Family ?Castoridae Gray, 1821
## Genus *Pipestoneomys* Donohoe

### *Pipestoneomys bisulcatus* Donohoe

*Pipestoneomys bisulcatus* Donohoe, 1956.

TYPE: CNHM UM 409, partial right maxilla with $M^1$-$M^3$.

HYPODIGM: CNHM UM 408, partial right mandible with $dP_4$-$M_1$ and CM 10047, partial left mandible with $P_4$-$M_1$.

DIAGNOSIS: "Cheek teeth high crowned, rooted, lacking prominent styles or stylids. $M^1$ and $M^2$ approximately equal in size, quadrangular; $M^3$ smaller, subcircular. Hypocone and protocone of $M^1$ and $M^2$ subequal, separated by a deep persistent groove. Deep groove separating anteroloph and paracone. Trigonid and talonid separated by a deep persistent groove, mesoconid well developed." (Donohoe, 1956: 264).

DESCRIPTION: The upper dentition has been thoroughly described by Donohoe. Consequently only certain features of the mandible and of $P_4$, material which was not available to him, will be described here.

The mandible is shallow but very thick below $P_4$-$M_1$. The masseteric fossa terminates under the midpoint of $P_4$ and its anterior border is rounded. The mental foramen lies immediately anterior to $P_4$ and about one-third of the way down the side of the jaw.

The incisor is triangular in cross section with a short, slit-like pulp cavity. Enamel is restricted to the slightly convex anterior face of the tooth. $P_4$-$M_1$ are badly worn in CM 10047, and little of the crown pattern is preserved. At this stage of wear $P_4$ shows two isolated lakes, one antero-internal, the other postero-internal, and a prominent buccal reentrant which persists to the base of the crown. $P_4$ is longer than is $M_1$.

MEASUREMENTS IN MILLIMETERS

CM 10047

| | | | | | |
|---|---|---|---|---|---|
| $P_4$ | a-p | 2.1 | $M_1$ | a-p | 1.7 |
| | tr. | 1.9 | | tr. | 1.8 |

AFFINITIES: *Pipestoneomys* was originally referred to the Aplodontidae (Donohoe, 1956), but recently, Alf (1962) while describing a new species of *Pipestoneomys, P. pattersoni,* has tentatively suggested castorid affinities for the genus. The absence of $P^3$ in *P. pattersoni,* as discussed by Alf, would tend to remove *Pipestoneomys* from the Aplodontidae, as would a number of characters seen in the upper dentition. However, the complete absence of any lingual folds on $P_4$ and $M_1$ argues

against castorid affinities, as does the absence of a hypoflexus in the upper cheek teeth.

The reference of *Pipestoneomys* to the ?Castoridae is extremely dubious and the genus will probably prove to be referable to neither the Aplodontidae nor the Castoridae. However, until more is known of this form it is here retained in the ?Castoridae, primarily to avoid further confusion in the literature.

## Family EOMYIDAE Depéret and Douxami, 1902

Five species of eomyids occur in the Pipestone Springs fauna. The relationships of these forms to each other and to other late Eocene and early Oligocene members of the family are considered below after the systematic section.

### Genus *Adjidaumo* Hay

#### *Adjidaumo minimus* (Matthew)
#### Figures 5e, 6b

*Gymnoptychus minimus* Matthew, 1903.
*Adjidaumo minimus* Wood, 1937.

TYPE: AMNH 9625, left mandible with $P_4$-$M_3$, angle, condyle and coronoid process missing.

REFERRED SPECIMENS: CM 9213, partial right mandible with $P_4$-$M_2$; CM 9214, partial right mandible with $P_4$-$M_3$; CM 10135, $LP_4$-$M_2$.

DIAGNOSIS: Smaller than *Adjidaumo minutus*, near size of *A. douglassi*; $P_4$-$M_3$ lower crowned than in *A. douglassi* with lophs not as high and prominent; posterior cingulum shorter and more compressed than in *A. douglassi*.

DESCRIPTION: The mandible is long and slender with the length of the diastema about one-quarter shorter than the length of the tooth row. The mental foramen lies anterior to $P_4$ and almost on the dorsal surface of the mandible. Below the posterior end of $P_4$ the masseteric fossa ends rather acutely in a large prominence. The dorsal masseteric ridge is stronger than the ventral and rises gently to the ascending ramus which originates opposite the posterior half of $M_2$. There is a prominent, elevated cap well up the lateral face of the ascending ramus marking the pulp cavity of the incisor much as in geomyids.

The lower incisor is compressed transversely with rounded anterior and lateral faces. The enamel extends just over the medial margin while laterally it covers half of the side of the tooth. The pulp cavity is narrow.

The protoconid and metaconid of $P_4$ are of equal size and are joined posteriorly by a short crest. The anterior valley between the cusps is open. In the four specimens available there is considerable variation in the transverse extent of the mesolophid. In the type and in CM 10135 the mesolophid is short and merges into the internal base of the metaconid while in CM 9214 it reaches almost to the lingual border and is free. In CM 9213 the mesolophid meets the base of the metaconid, where it is joined by a short crest from the lingual border, which may represent an elongate mesostylid although no trace of this cusp can be seen in any of the other specimens available. The ectolophid of $P_4$ is short, and there is no indication of a mesoconid. The posterior cingulum is extremely short, arising from the midpoint of the hypolophid and fading into the postero-internal base of the entoconid.

The molars present more or less the same crown pattern as the premolars, with $M_1$-$M_2$ being of nearly equal size and $M_3$ smaller. The anterior cingulum is joined to the base of the metaconid and by a short crest to the metalophid where the latter leaves the protoconid. The buccal end of the cingulum is free. The mesolophid is longer on $M_2$ and $M_3$ than on $M_1$ in the type and CM 10135, but it is of the same length on $M_1$-$M_2$ in CM 9213 and CM 9214. In the type the mesolophids are free at their lingual ends, but in the other specimens they reach the base of the entoconids. The posterior cingulum is better developed on $M_1$ than on $M_2$ and is absent on $M_3$. As a result the valley between the posterior cingulum and entoconid is wider on $M_1$ than on $M_2$.

<div align="center">MEASUREMENTS IN MILLIMETERS</div>

| | AMNH 9625 | CM 9213 | CM 9214 | CM 10132 |
|---|---|---|---|---|
| Alveolar length   $P_4$-$M_3$ | 3.6 | 3.8 | 3.8 | 4.2 |
| Length of diastema | 3.0 | 3.0 | 3.0 | 3.0 |
| Depth below $M_1$ | 2.6 | — | — | 2.8 |
| $P_4$    a-p | .8 | .8 | .8 | .8 |
|   tr. | .7- .8 | .6- .7 | .6- .8 | .7- .8 |
| $M_1$    a-p | .9 | 1.0 | 1.0 | .9 |
|   tr. | .9- .9 | .9- .9 | .9- — | .9- .9 |
| $M_2$    a-p | .9 | 1.0 | 1.0 | .9 |
|   tr. | 1.0- .9 | 1.0-1.0 | 1.0-1.0 | 1.0- .9 |
| $M_3$    a-p | .9 | — | .9 | — |
|   tr. | .9- .7 | — | .8- .8 | — |
| $I_1$    a-p | .9 | — | — | — |
|   tr. | .6 | — | — | — |

## Genus *Paradjidaumo* Burke

### *Paradjidaumo minor* (Douglass)
### Figure 4

*Eumys minor* Douglass, 1901
*Gymnoptychus minor* (Douglass), Matthew, 1903.
*Adjidaumo minor* (Douglass), Hay, 1930.
*Paradjidaumo minor* (Douglass), Burke, 1934.

TYPE: CM 735, a partial right mandible with $P_4$-$M_1$.

REFERRED SPECIMENS: Eighty-six specimens in the collections of Carnegie Museum and numerous other specimens in the AMNH, USNM, and CNHM collections.

DIAGNOSIS: Somewhat smaller than *P. trilophus;* cheek teeth lower crowned; anterior cingulum of $M_1$-$M_3$ not as closely appressed to metalophid; mesolophid generally long, reaching lingual border of $P_4$-$M_3$.

DESCRIPTION: There is only one skull fragment in the present collection which can be assigned to *P. minor*. The anterior portion of the skull is preserved from the posterior alveolar border forward and agrees in most details with the condition described by Wilson (1949) for a skull of *P. trilophus*. There is a rather large, shallow depression above the infraorbital foramen and passing forward to the premaxillary-maxillary suture from which a portion of the *masseter lateralis* probably arose. Prominent premaxillary ridges are also present lateral to the incisors. The maxillary-palatine suture lies somewhat farther forward in *P. minor* than in *P. trilophus,* terminating opposite the middle of $P_4$ in the Pipestone Springs species. In other details the skull of *P. minor* appears identical to that of *P. trilophus*.

The cheek teeth of *Paradjidaumo* are mesodont, showing in relation to other eomyids an increase in the height of the cross lophs and lophids as well as increase in height of cusps. The teeth of *P. minor* are somewhat less advanced in this character than are those of *P. trilophus* but the difference is not great. There is considerable variation in occlusal pattern in the Pipestone Springs material, particularly in $P^4/_4$ and $M^3/_3$.

The fourth upper premolar is essentially molariform, differing from $M^1$-$M^2$ primarily in the absence of the anterior cingulum. In CM 9231, however, there is a very shallow, compressed pocket on the anterior face of the paracone which is bounded anteriorly by what is probably a short anterior cingulum that fades into the anterior face of the paracone. This pit would be obliterated with further wear. In other unworn specimens such as CM 8979 (fig. 4e), and in all other worn specimens

there is no trace of an anterior cingulum. The mesoloph on $P^4$ is variable in length, reaching across the crown surface to the mesostyle in CM 9231 but ending in the center of the crown in CM 8979 and CM 9896. The valley between the metaloph and posterior cingulum is moderately deep and these elements become fused into a single loph only after considerable wear.

The first upper molar is the largest of the cheek teeth but it differs only slightly from $M^2$ in crown pattern. The anterior cingulum is distinct on both $M^1$-$M^2$ when the teeth are unworn, but it quickly merges with the protoloph as wear proceeds. The posterior cingulum remains distinct somewhat longer but it also eventually fuses with the metaloph, producing the "Omega" pattern. The mesoloph joins a short spur from the mesostyle to form a complete loph across the center of $M^1$ in all the specimens available. In $M^2$, however, the mesoloph does not reach the mesostyle in CM 8979 so that no complete central loph is formed. In some specimens the two elements are joined in the unworn state, while in others they become fused only after moderate wear has occurred.

The third upper molar is the smallest of the upper cheek teeth and the crown elements are reduced. The protocone and paracone are the largest cusps and they are joined by a strong protoloph. The anterior cingulum is short and is confined to the buccal quarter of the anterior face of the tooth. The elements behind the protoloph are variable in their development. In CM 9231 the hypocone and metacone are distinct and moderately large and there is a small lingual valley between the protocone and hypocone. In CM 8979 the hypocone and metacone are small and there is only a faint cleft between the lingual cusps. In CM 8979 there is a well developed mesoloph passing from the postero-internal corner of the protocone obliquely across the crown to a large mesostyle; while in CM 9271 the mesoloph is shorter and arises from the midpoint of the metaloph, passing anteriorly and then buccally to the mesostyle. The posterior cingulum is generally very short.

The superior incisors are transversely compressed, ungrooved, and have slightly rounded anterior and lateral faces. The pulp cavity is a short, narrow slit.

The mandible of *Paradjidaumo* is larger but of the same type as that of *Adjidaumo*. It is long and slender with a V-shaped masseteric fossa extending forward under $P_4$, a long diastema, mental foramen lying high on the side of the jaw midway between the incisor and premolar, and a pronounced rounded expansion on the lateral side of the ascending ramus marking the pulp cavity of the incisor. The condyle lies above

the tooth row, is elongate antero-posteriorly, and faces upward and outward.

The deciduous lower premolars are more slender than $P_4$, but in other details the teeth agree fairly closely. The trigonid is higher than the talonid, with the protoconid and metaconid closely appressed and joined by a very short posterior protoconid arm. A short anterior cingulum is present in some specimens and absent in others. When present it drops sharply from the anterior face of the protoconid to merge into the base of the metaconid. In some specimens a distinct trigonid pit is isolated between the anterior cingulum and protoconid arm, while in others the trigonid basin is open anteriorly. The length of the mesolophid is also variable. In many specimens it reaches the lingual margin while in some it passes only three-quarters of the way across the crown. The presence or absence of a posterior cingulum is also variable but when present it is short. The hypolophid passes from the entoconid to the posterolophid rather than to the hypoconid.

When unworn, $M_1$ and $M_2$ show a five-crested pattern which changes with wear to a three-crested pattern. The anterior cingulum is longer than the posterior and set off more distinctly from the metalophid than the posterior cingulum is from the hypolophid. As in the premolar, the length of the mesolophid is variable but it always passes at least half-way across the occlusal surface. The posterior elements of $M_3$ are reduced through the lateral compression of the hypoconid and entoconid and the loss of the posterior cingulum.

The lower incisors are transversely compressed and have flat anterior and convex lateral faces. There is a low ridge along the lateral margin of the external face. The enamel extends about halfway up the lateral face. The pulp cavity is slit-like.
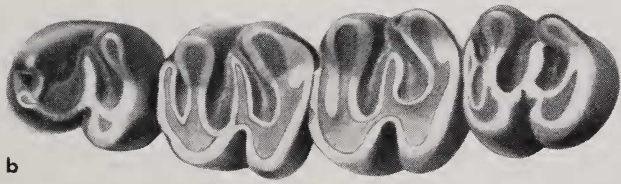
MEASUREMENTS IN MILLIMETERS

| | Number of Specimens | Mean | Standard Deviation | Coefficient of Variation | Observed Range |
|---|---|---|---|---|---|
| Alveolar length   $P^4$-$M^3$ | 4 | 5.2 | — | — | 4.7-5.8 |
| Alveolar length   $P_4$-$M_3$ | 49 | 5.7 | .34 | 6.0 | 5.2-6.6 |
| Length of diastema | 33 | 4.8 | .40 | 8.3 | 4.0-6.0 |
| Depth below $M_1$ | 53 | 3.8 | .19 | 3.6 | 3.4-4.5 |

Fig. 4   *Paradjidaumo minor.* **a.** CM 10051, left mandible, x5. **b.** Same, LP$_4$-M$_3$, x15. **c.** CM 10041, RdP$_4$-M$_2$, x15. **d.** CM 9231, LP$^4$-M$^3$, x10. **e.** CM 8979, RP$^4$-M$^3$, x15.
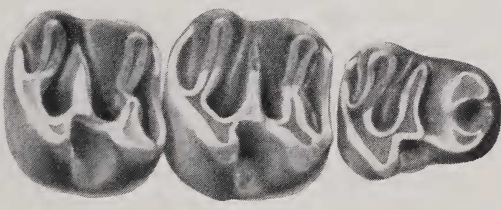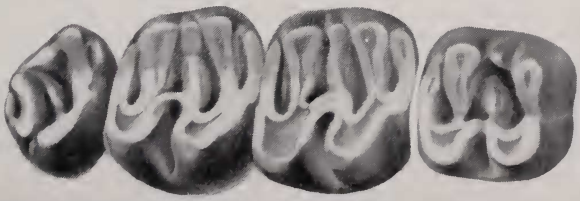
| | | | Number of Specimens | Mean | Standard Deviation | Coefficient of Variation | Observed Range |
|---|---|---|---|---|---|---|---|
| $P^4$ | a-p | | 7 | 1.3 | — | — | 1.1-1.5 |
| | tr. | | 7 | 1.4 | — | — | 1.2-1.6 |
| $M^1$ | a-p | | 8 | 1.4 | — | — | 1.4-1.5 |
| | tr. | | 8 | 1.6 | — | — | 1.4-1.7 |
| $M^2$ | a-p | | 8 | 1.3 | — | — | 1.2-1.4 |
| | tr. | | 8 | 1.6 | — | — | 1.6-1.7 |
| $M^3$ | a-p | | 6 | .9 | — | — | .8-1.0 |
| | tr. | | 6 | 1.3 | — | — | 1.2-1.4 |
| $I^1$ | a-p | | 1 | 1.7 | — | — | — |
| | tr. | | 1 | 1.0 | — | — | — |
| $P_4$ | a-p | | 30 | 1.41 | .11 | 3.6 | 1.1-1.6 |
| | tr. | metalophid | 30 | 1.36 | .12 | 8.8 | 1.0-1.5 |
| | tr. | hypolophid | 30 | 1.05 | .09 | 8.5 | .9-1.3 |
| $M_1$ | a-p | | 36 | 1.44 | .09 | 6.1 | 1.3-1.6 |
| | tr. | | 36 | 1.51 | .91 | 6.0 | 1.3-1.7 |
| $M_2$ | a-p | | 33 | 1.38 | .07 | 4.9 | 1.2-1.5 |
| | tr. | | 33 | 1.54 | .08 | 5.4 | 1.4-1.7 |
| $M_3$ | a-p | | 16 | 1.29 | .14 | 11.0 | 1.1-1.5 |
| | tr. | | 16 | 1.34 | .08 | 6.0 | 1.2-1.5 |
| $I_1$ | a-p | | 17 | 1.50 | .03 | 1.8 | 1.3-1.6 |
| | tr. | | 17 | 0.98 | .02 | 1.6 | 0.9-1.0 |

## Genus *Yoderimys* Wood

### Yoderimys burkei[1], new species

### Figures 5i, 6a

TYPE: CM 9782, partial left mandible with $P_4$-$M_2$, lacking ascending ramus and angle.

HYPODIGM: Type only.

DIAGNOSIS: Larger than *Yoderimys bumpi*; mandible short, extremely heavy; diastema short, deep; cheek teeth brachydont; $P_4$ as large as $M_1$-$M_2$; anteroconid present on $P_4$; anterior cingulum on $M_1$-$M_2$ wide, free both buccally and lingually; long lophid passes from center of anterior cingulum to center of metalophid on $M_1$-$M_2$; mesolophid long, directed anteriorly to base of metaconid; hypolophid arises at antero-internal corner of hypoconid on $P_4$-$M_2$; posterior cingulum of $P_4$-$M_2$ expanded.

[1] The specific name is given in honor of J. J. Burke for his work on early Oligocene rodents and rabbits.

DESCRIPTION:    The jaw is short, deep and very heavy. Anterior to $P_4$ the dorsal surface of the mandible drops rather steeply and then turns upward in a gentle slope to the rear of the incisor. The mental foramen lies below the anterior root of $P_4$ about one-quarter of the way down the side of the ramus. The masseteric fossa ends in a semicircular depression below the contact of $P_4$ and $M_1$, whereas in *Y. bumpi* it reaches somewhat farther forward. The dorsal masseteric crest cuts off this anterior depression from the main extent of the fossa as it passes obliquely down the lateral side of the ramus to fuse with the ventral ridge below the middle of $M_1$. Although most of the ascending ramus is missing it appears to arise much farther down on the side of the mandible than in other eomyids, with its anterior border rising well below $M_2$.

The cheek teeth are brachyodont. Although all are well worn so that most of the detail of the crown pattern is lost on the anterior half of $P_4$, the arrangement of the lophids is still plain on the posterior half of $P_4$ and on $M_1$-$M_2$. The anterior half of $P_4$ is slightly compressed transversely. The lower premolars of *Y. bumpi* and *Y. burkei* are similar in most respects, but the anteroconid is smaller in *Y. bumpi*. It is connected to the protoconid by a narrow lophid but is completely separated from the metaconid. The protoconid-metaconid connections and the position of the mesolophid have been obliterated by wear, although there is some indication that the mesolophid passed obliquely forward to fuse with the base of the metaconid. The hypoconid on $P_4$ lies somewhat behind the entoconid, and the cusps are joined by a lophid arising from the center of the entoconid and joining the anterior hypoconid arm where the latter meets the ectolophid. The posterior cingulum passes lingually to the base of the entoconid but fails to reach the lingual margin of $P_4$. The valley between the entoconid-hypolophid and the posterior cingulum is narrow and shallow. The buccal valley between the protoconid and hypoconid is wide and deep, with the ectolophid passing along the midline of the tooth.

The crown patterns of $M_1$-$M_2$ are essentially identical. The protoconids and hypoconids lie slightly behind the metaconids and entoconids so that the transverse lophids cross from the center of the lingual cusps to the anterior corners of the buccal cusps. The metalophids are stronger than in *Y. bumpi*. The ectolophid lies along the midline of $M_1$-$M_2$ as it does on $P_4$ and is more internal in position than in *Y. bumpi*. The buccal valley is wide. The mesolophid passes to the base of the metaconid internal to the lingual margin of $M_1$-$M_2$ and is in general longer than in the Wyoming species. On both teeth the portion anterior to the

metalophid is expanded antero-posteriorly into a wide shelf, which is divided into buccal and lingual areas by a strong anteroposterior lophid. This lophid arises from the anterior face of $M_1$-$M_2$ and passes into the middle of the metalophid. The anterior border of $M_1$-$M_2$ is elevated into a thin transverse ridge which is somewhat stronger on $M_2$. The posterior cingulum is slightly elevated on $M_1$-$M_2$, and fuses with the base of the entoconid, thus enclosing a rather wide valley between the cingulum and the hypolophid.

<div align="center">MEASUREMENTS IN MILLIMETERS</div>

<div align="center">CM 9782</div>

| | | | | |
|---|---|---|---|---|
| Length of diastema | 5.6 | $M_1$ | a-p | 2.3 |
| Depth below $M_1$ | 5.8 | | tr. | 1.8-1.9 |
| $P_4$   a-p | 2.3 | | | |
|     tr. | 1.7-2.0 | $M_2$ | a-p | 2.3 |
| | | | tr. | 2.0-2.0 |

## Namatomys, new genus

### Type species: Namatomys[1] lloydi[2], new species

DIAGNOSIS: Near size of *Adjidaumo;* mandible short, deep; diastema short; $P_4$ with small anteroconid; anterior cingulum free buccally on $P_4$-$M_3$, joins anterior protoconid arm on $M_1$-$M_3$; anterior and posterior protoconid arms present on $P_4$-$M_3$, both fused to base of metaconid; ectolophid long, set well in towards center of $P_4$-$M_3$; mesolophid very short, directed towards hypolophid; hypolophid passes to hypoconid on $P_4$, hypoconulid on $M_1$-$M_2$; posterior half of $M_3$ only partially reduced.

### Namatomys lloydi, new species
### Figures 5c,d; 6d

TYPE: CM 8976, partial left mandible with $P_4$-$M_3$, lacking ascending ramus, angle and part of incisor.

HYPODIGM: Type and CM 10046, partial left ramus with $P_4$-$M_2$.

DIAGNOSIS: Only known species of the genus.

[1] From Greek *nama, namatos,* spring or stream and *mys* mouse.

[2] The specific name is given in honor of Mr. A. C. Lloyd, who spent many seasons collecting with Dr. J. L. Kay at Pipestone Springs.

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Fig. 5   **a-b.** *Aulolithomys bounites,* new genus and species. **a.** USNM 22825, $RP_4$-$M_3$, x10. **b.** USNM 20974, Type, $LP_4$-$M_2$, v10. **c-d.** *Namatomys lloydi,* new genus and species. **c.** CM 8976, $LP_4$-$M_3$, Type, x10. **d.** CM 10046, $LP_4$-$M_2$, x10. **e.** *Adjidaumo minimus,* AMNH 9625, $LP_4$-$M_3$, Type, x15. **f-h.** *Heliscomys* cf. *H. vetus,* **f.** CM 9006, $LP^1$-$M^3$, x15. **g.** CM 9230, $LP_4$-$M_1$, x15. **h.** CNHM PM 8627, $LP_4$-$M_1$, x15. **i.** *Yoderimys burkei,* new species. CM 9782, $LP_4$-$M_2$, Type, x10.
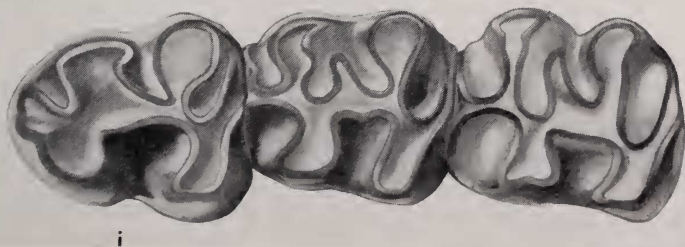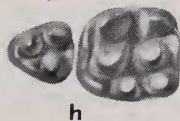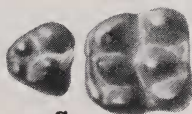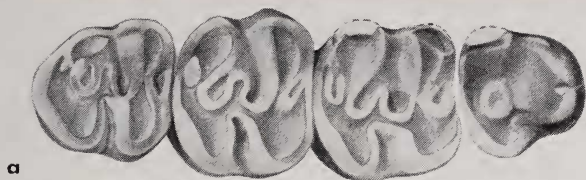
DESCRIPTION: The mandible is short and deep with the diastemal length less than the alveolar length of $P_4$-$M_3$. The anterior surface of the mandible drops abruptly anterior to $P_4$ and then rises gently to the incisor alveolus with the anterior tip of the mandible lying at the same level as the $P_4$-$M_3$ alveoli. The mental foramen lies just below the dorsal border of the mandible and slightly anterior to $P_4$. The masseteric fossa is delimited by strong dorsal and ventral ridges and extends forward below the posterior half of $P_4$.

The lower incisors are compressed transversely and have rounded anterior and lateral faces. The enamel extends over about one-third of the lateral surface but does not overlap onto the medial side of the tooth. The pulp cavity is narrow and slit-like.

The cheek teeth are brachyodont with high principal cusps and low lophs; they are essentially equal in their anteroposterior dimensions but $P_4$ is narrower than are $M_1$-$M_3$. All of the teeth show the presence of two protoconid arms which pinch into the base of the metaconid, isolating a small, circular pit between the protoconid and metaconid. The strength of the anterior protoconid arm varies on $P_4$ in the two specimens available, being stronger on the type than on CM 10046. On all cheek teeth the ectolophid is long and set in from the buccal margin about one-third of the distance across the tooth. The buccal valley is therefore deep and is squared off internally.

There is a small anterior cingulum on $P_4$ which is better developed in CM 8976 than in CM 10046. The protoconid and metaconid are set close together, leaving only a very small pit isolated between the cusps and the protoconid arms. The mesolophid on $P_4$ is extremely short in both specimens. The hypolophid arises at the postero-internal corner of the hypoconid and is directed slightly anteriorly to the corner of the entoconid. The posterior cingulum is short on $P_4$, failing to reach the lingual border of the tooth, and the valley between the hypolophid and posterior cingulum is very narrow.

Though nearly identical in crown pattern, $M_1$-$M_2$ differ in the shorter and more acutely angled hypolophid on $M_2$. On $M_2$, the hypolophid arises from the midpoint of the posterior border, while on $M_1$ it arises much closer to the hypoconid. In both teeth the anterior cingulum reaches completely across the anterior face, fusing with the base of the metaconid internally but remaining free externally. The cingulum is connected to the anterior protoconid arm at the antero-internal corner of the protoconid. The mesolophid is very short on both $M_1$-$M_2$ but is slightly longer on $M_2$ than on $M_1$.

The anterior half of $M_3$ does not differ from the condition seen in $M_1$-$M_2$, but there is some reduction in the posterior half of the tooth. The entoconid is not recognizable as a distinct cusp but is fused into a wide, heavy posterior ridge within which the hypolophid and posterior cingulum are also indistinguishable. The ectolophid is shorter on $M_3$ and not as high as it is on $M_1$-$M_2$. The mesolophid is longer on $M_3$ than on $M_1$-$M_2$.

MEASUREMENTS IN MILLIMETERS

|  |  | CM 8976 | CM 10046 |
|---|---|---|---|
| Alveolar length $P_4$-$M_3$ |  | 5.2 | 5.0 |
| Length of diastema |  | — | 3.7 |
| Depth below $M_1$ |  | 3.8 | 3.8 |
| $P_4$ | a-p | 1.3 | 1.3 |
|  | tr. | 1.0-1.1 | 1.0-1.1 |
| $M_1$ | a-p | 1.4 | 1.4 |
|  | tr. | 1.3-1.3 | 1.3-1.3 |
| $M_2$ | a-p | 1.4 | 1.4 |
|  | tr. | 1.4-1.4 | 1.3-1.3 |
| $M_3$ | a-p | 1.3 | — |
|  | tr. | 1.3-1.1 | — |
| $I_1$ | a-p | — | 1.5 |
|  | tr. | — | 0.9 |

## Aulolithomys, new genus

Type species: **Aulolithomys[1] bounites[2]**, new species

DIAGNOSIS: Larger than *Adjidaumo, Paradjidaumo.* and *Namatomys;* smaller than *Centimanomys;* cheek teeth brachyodont; $P_4$ compressed antero-posteriorly; metaconids and entoconids of $M_1$-$M_2$ set close together; molars not as elongate in relation to width as in other North American eomyids; anterior and posterior cingula short on $P_4$-$M_2$; when unworn, buccal end of anterior cingulum free on $M_1$-$M_2$; mesolophids short and low; metaconids elongate antero-posteriorly on $P_4$-$M_3$.

## Aulolithomys bounites, new species
### Figures 5a,b;6c

TYPE: USNM 20974, left mandible with $P_4$-$M_2$, missing $M_3$, angle, coronoid process, and condyle.

[1] From Greek *aulon, os* pipe, *lithos* stone, and *mys* mouse, pipestone mouse.
[2] From Greek *bounites,* dweller in the hills.

HYPODIGM: Type and USNM 22825, right mandible with worn $P_4$-$M_3$. CM 9780, partial left mandible with $P_4$-$M_2$, and CM 10099, fragment of left mandible with $M_1$.

DIAGNOSIS: Only known species of genus.

DESCRIPTION: The mandible resembles that of *Adjidaumo* and *Paradjidaumo* but is considerably larger than in those genera. The diastema is long, its length nearly equaling the alveolar length of $P_4$-$M_3$. The mental foramen lies just below the dorsal surface of the diastemal portion of the mandible and just anterior of $P_4$. The masseteric fossa is deeply concave with prominent dorsal and ventral masseteric ridges. The ventral masseteric ridge extends forward under the anterior end of $P_4$ and the dorsal ridge terminates below the anterior end of $M_1$, thus failing to join the ventral ridge and close the masseteric fossa anteriorly. The ascending ramus rises rather steeply beginning opposite the middle of $M_2$. The incisor pulp cavity forms a rounded prominence on the ascending ramus.

The lower incisor is compressed laterally with a nearly flat anterior face and a rounded lateral margin. The enamel covers half of the lateral surface and overlaps very slightly onto the medial side of the tooth. The pulp cavity is a short, narrow slit on the wear surface.

The fourth lower premolar is small, more so than in any eomyid other than *Rhodanomys* with which I am familiar. The protoconid and entoconid are separated by a very small, shallow trigonid basin, but with little wear they become fused into a single, heavy ridge. When unworn these cusps are joined by a short anterior cingulum and metalophid, which enclose the trigonid basin. There is a short, low mesolophid that fades into the talonid basin at the center of the tooth. The hypoconid and entoconid are united through the posterior cingulum. The hypolophid passes from the hypoconid to the midpoint of the posterior edge of the tooth where it meets an arm from the entoconid. The posterior cingulum proceeds lingually from this point to fuse with the posterior margin of the entoconid.

The first and second lower molars are subequal in size and rectangular in occlusal outline. When unworn the anterior cingulum was probably free at the buccal margin on each tooth, but this condition is seen

Fig. 6  **a.** *Yoderimys burkei*, CM 9782, lateral view left mandible, Type, x7½. **b.** *Adjidaumo minimus*, AMNH 9625, lateral view left mandible, Type, x10. **c.** *Aulolithomys bounites*, USNM 22825, lateral view right mandible, x5. **d.** *Namatomys lloydi*, CM 10046, lateral view left mandible, x10.

only on $M_2$ of the type specimen in the material available. Lingually, the cingulum fuses with the base of the metaconid before reaching the lingual margin. It is also joined to the antero-internal corner of the protoconid on both $M_1$-$M_2$. All the lophids on $M_1$-$M_2$ are low; the metalophid passes directly across the crown while the posterior lophid shows the same condition described for $P_4$. On both $M_1$-$M_2$ the mesolophid is short, reaching only to the middle of the talonid basin. The metaconids are expanded with elongate posterior buttresses which probably represent a fusion of the mesostylids with the metaconid slopes. These buttresses reach the entoconids near their bases. The posterior cingulum is short and fuses with the entoconid as in $P_4$.

The only third lower molar is too worn to show much of the crown pattern. As in $M_1$-$M_2$ the mesolophid is short, the metalophid straight, and the buccal end of the anterior cingulum was probably free at an early wear stage. The posterior half of $M_3$ is reduced, the entoconid being set close to the metaconid, and the hypolophid shortened.

MEASUREMENTS IN MILLIMETERS

| | | CM 9780 | CM 10099 | USNM 22825 | USNM 20974 |
|---|---|---|---|---|---|
| Alveolar length | $P_4$-$M_3$ | — | — | 7.2 | 6.8 |
| Length of diastema | | 6.2 | — | 6.3 | 6.3 |
| Depth below $M_1$ | | 5.3 | — | 5.5 | 4.7 |
| $P_4$ | a-p | 1.5 | — | 1.6 | 1.6 |
| | tr. | 1.2-1.7 | — | 1.3-1.7 | 1.3-1.7 |
| $M_1$ | a-p | 1.8 | 1.8 | 1.9 | 1.7 |
| | tr. | 1.8-2.0 | 1.9-2.0 | 1.9-2.0 | 1.8-1.8 |
| $M_2$ | a-p | 1.8 | — | 1.9 | 1.6 |
| | tr. | 2.0-2.0 | — | 2.1-2.1 | 1.9-2.0 |
| $M_3$ | a-p | — | — | 1.8 | — |
| | tr. | — | — | 2.1-2.1 | — |
| $I_1$ | a-p | 2.0 | — | 2.0 | 2.0 |
| | tr. | 1.3 | — | 1.2 | 1.2 |

## RELATIONSHIPS OF NORTH AMERICAN EOMYIDS

The last review of North American eomyids was that by Wilson (1949: 112-114). At that time only three early Teritary North American genera were known: *Protadjidaumo* from the Duchesnean late Eocene, and *Adjidaumo* and *Paradjidaumo* from the Oligocene. Since then Gal-

breath (1955) has described a fourth genus, *Centimanomys*, from the early Chadronian of northeastern Colorado, and stated that it was unlike other known eomyids in a number of dental characters but that it might be related to an undescribed form from the early Oligocene of Texas. In the same year, Wood (1955) described another new genus, *Yoderimys*, from the early Oligocene of Goshen Hole, Wyoming, and also compared it with the undescribed Texas form, erecting a new sub-family, the Yoderimyinae for *Yoderimys* and the Texas species. In the present paper, two new genera of eomyids, *Namatomys* and *Aulolith-omys*, have been described as well as a second species of *Yoderimys*, thus bringing the total number of eomyid genera now recognized from the late Eocene and early Oligocene to seven.

Of these seven genera, three, *Protadjidaumo*, *Adjidaumo*, and *Par-adjidaumo*, are obviously closely related as has been shown by Burke (1934). *Adjidaumo* was probably descended from *Protadjidaumo* although not from *Protadjidaumo typus*. The cheek teeth of the Duches-nean species are higher crowned and the lophids are stronger than in *Adjidaumo*, thus making *P. typus* too advanced to be directly ancestral to *Adjidaumo*. The cheek teeth of *Paradjidaumo* are much higher crown-ed and the lophs and lophids are more prominent than in either *Adjid-aumo* or *Protadjidaumo*, but the patterns are essentially similar, and it is probable that *Paradjidaumo* and *Protadjidaumo* had a common ancestor in the Uintan. It is also probable that these genera are closely related to *Eomys* of the late Eocene of Europe.

The relationships of the other five early Oligocene genera to *Prot-adjidaumo*, *Adjidaumo*, and *Paradjidaumo*, and to each other, are un-certain. The presence of $P^3$ in *Yoderimys bumpi* from eastern Wyoming, is unique among all eomyids for which the upper dentition is known; and this, together with unusual loph and lophid developments on $P^4/_4$-$M^3/_3$, removes *Yoderimys* from any close relationship with other eomyids. *Yoderimys burkei* from Pipestone Springs, while known only from the lower dentition, appears to be closely related to the Wyoming species. The large anteroconid on $P_4$, short mesolophid on $P_4$-$M_3$, em-phasis on cusps rather than lophids, and anterior position of the hypo-lophid all support this relationship. Although both *Yoderimys* and *Centimanomys* have at least tentatively been compared with the un-described Texas eomyid, they do not appear to be closely related to each other. The transverse lophids on $P_4$-$M_3$ are extremely prominent in *Centimanomys* while the reverse condition is seen in *Yoderimys*. This emphasis on the lophids, together with the brachyodont condition

of the cheek teeth and the narrow trigonid of $P_4$, isolates *Centimanomys* as another separate eomyid line with no known ancestor or descendants.

This same isolated position within the family seems to hold true also for the new Pipestone Springs genera described above. There is possibly some indication of relationship of *Aulolithomys* to *Centimanomys* in the structure of $P_4$. The narrow trigonid with near fusion of protoconid and metaconid is known only in these two genera among North American eomyids. However, in *Aulolithomys* there has been little emphasis on the development of the strong transverse lophids which are so prominent in *Centimanomys*, and the jaw proportions are rather different, with the diastemal length approaching the alveolar length in *Aulolithomys* (ratio .90), while the diastema length is considerably less than the alveolar length in *Centimanomys* (ratio .71). There is some resemblance between *Aulolithomys* and the early Aquitanian European *Rhodanomys* as figured by Stehlin & Schaub (1951, fig. 505), particularly in the narrow trigonid of $P_4$ and greatly reduced to absent mesolophid on $P_4$-$M_3$. *Rhodanomys*, however, appears to be higher crowned than *Aulolithomys* and also differs from *Aulolithomys* in the great reduction of the anterior cingulum on $M_1$-$M_3$ and the apparent loss of the posterior cingulum.

The relationships of the second new Pipestone form, *Namatomys*, are also obscure. No other member of the Eomyidae displays two protoconid-metaconid crests on $P_4$-$M_3$, features that are so prominent in *Namatomys*. In some features, such as the cuspate rather than lophate condition, the free anterior cingulum, and unreduced $P_4$, *Namatomys* appears to be rather close to *Protadjidaumo* and *Adjidaumo*. However, the double metalophid condition would appear to me to be of rather fundamental importance, thus removing *Namatomys* from any close relationship to the other early Oligocene eomyids.

The number and diversity of eomyids now known from the early Oligocene would seem to indicate either a much greater late Eocene radiation in North America than has been recognized to date or a considerable immigration into western North America in the latest Eocene from some other center of radiation. Three species are known from the late Eocene or early Oligocene of British Columbia but these are all of the more typical *Adjidaumo-Paradjidaumo* stock and give no information as to the possible ancestry or relationships of *Namatomys, Aulolithomys, Centimanomys* or *Yoderimys*. No European eomyids, other than *Eomys*, are at present known from the late Eocene; the major Old World eomyid radiation evidently took place during the Aquitanian

and Burdigalian. Thus no late Eocene eomyids are now known which could have been ancestral to four of the species in the North American early Oligocene.

It is of some interest to note that five species of eomyids belonging to five genera are present in the Pipestone Springs fauna. Four of these species are represented by no more than four specimens, while *Paradjidaumo minor* is known from more than a hundred specimens. In the case of *Namatomys lloydi, Aulolithomys bounites,* and *Yoderimys burkei* this paucity probably indicates that these species were not members of the community living around the area of deposition. These species are all as large as, or larger than, *Paradjidaumo minor* and I would not expect sampling bias to play a part in their rare occurrence. The situation in regard to *Adjidaumo minimus* is not as clear. Only four individuals are known, but here small size may be responsible, at least in part, for the scarcity of this species in collections. The presence of such a large number of individuals of *Paradjidaumo minor* makes it rather certain that this species was living around the area of deposition.

As Wilson (1949: 112) has pointed out, the tooth pattern in eomyids is similar to, although not identical with, the cricetodont pattern. It is quite possible that members of the Eomyidae occupied many of the same habitats that were later filled by the cricetids. No members of the Cricetidae are at present definitely known from the early Oligocene. Eumyine cricetids are abundant in the Orellan, however, and by the Arikareean, a number of cricetid types are known. The eomyids, on the other hand, appear to have had their major North American radiation during the late Eocene and early Oligocene with only *Adjidaumo* and *Paradjidaumo* persisting through the Oligocene. On the basis of occurrence it seems possible that many of the early Oligocene eomyids such as *Yoderimys, Centimanomys, Namatomys,* and *Aulolithomys* were replaced by the more highly specialized cricetids during Chadronian times.

Eomyids are known in North America after the Oligocene but they were evidently not abundant and the relationship of at least two of the later forms are unknown. The otherwise European genus, *Pseudotheridomys,* is represented in the North American early Miocene by *Pseudotheridomys hesperus* (Wilson, 1960) from the Martin Canyon Quarry A fauna. This species is closely related to European forms and evidently represents an early Miocene immigration into the New World. Two other forms are known from the Pliocene, both from single jaws. *Kansasimys dubius* (Wood, 1936) from the Hemphillian of Kansas, and

*Leptodontomys oregonensis* (Shotwell, 1956) from the Hemphillian of Oregon, are both tentatively referred to the Eomyidae. Their ancestry, however, is unknown.

Our knowledge of the family Eomyidae has increased considerably in the last decade, but an understanding of the evolution of many lines within the group will not be possible until further material is known from deposits of Uintan and Duchesnean age. The eomyids were probably descended from members of the Sciuravidae, sometime during the latter half of the Eocene, but these ancestors are not known as yet. In habitus many eomyids probably resembled cricetids and I think it is likely that they were replaced in large part by the latter.

Family HETEROMYIDAE Allen and Chapman, 1893
Genus *Heliscomys* Cope

*Heliscomys* cf. *H. vetus* Cope
Figures 5f-h

*Heliscomys vetus* Cope, 1873.

REFERRED SPECIMENS: CM 9006, fragment of left maxilla with $P^4$-$M^3$; CM 10101, fragment of left maxilla with $P^4$-$M^1$. CNHM UM 1643, $LP^4$. CM 9230, partial left mandible with $P_4$-$M_1$; and CNHM PM 8627, partial left mandible with $P_4$-$M_1$.

DESCRIPTION: The sample is much too small to show the probable range of variation present in this population, but it is interesting to note that some of the premolar variations discussed by Galbreath (1953: 63-64) for Orellan populations are seen also in the Pipestone material.

The upper premolars show a pattern of a large, anteriorly placed protocone and a three-cusped metaloph. The protocone, metacone, and hypocone are nearly of equal size and are high and sharp. There is little tendency in $P^4$ or in $M^1$-$M^3$ towards the formation of transverse lophs. The cusps are discrete and only at a very late wear stage would they lose their individual identity. The entostyle is a small, low cusp on $P^4$ in all specimens. In CM 9006 and 10101 there is no trace of a posterior cingulum connecting the bases of the hypocone and metacone; in CNHM UM 1643, the cingulum is present. At the antero-buccal base of the protocone there is a small cusp which is found in all specimens. The size of the cusp varies, however, being much larger in CM 9006 than in the other two specimens.

The first upper molar is the largest of the four cheek teeth. The protoloph is essentially two-cusped with the lingual extension of the anterior

cingulum forming a narrow ridge internal to the protocone and with no indication of a distinct protostyle. The central valley between protoloph and metaloph is deeper than the anteroposterior valleys and is open lingually. The metaloph is composed of three subequal cusps with the entostyle only slightly smaller than the hypocone and metacone. The valley between the entostyle and hypocone is not as deep as that between the hypocone-metacone and protocone-paracone. There is a short posterior cingulum which arises from near the base of the hypocone and passes to the buccal margin of the tooth.

The second upper molar agrees in most respects with the pattern seen on $M^1$; the differences lie in the construction of the lingual cingulum and the styles. On $M^2$ there is a high ridge which closes the central valley at the lingual margin. It is impossible to distinguish either a protostyle or entostyle in this ridge, but the connection to the anterior cingulum is stronger and at a higher level than is the connection to the hypocone.

The third upper molar is reduced and is composed of only two distinct cusps, the protocone and paracone, and a high internal ridge which is connected to the anterior and posterior cingulum. The metalophid is reduced and fused with the posterior cingulum and there is no trace of either the hypocone or metacone.

The mandible is rather slender but the anterior end of the masseteric fossa, at the junction of the dorsal and ventral masseteric ridges, is swollen and makes the jaw appear massive at this point. The masseteric fossa terminates under $P_4$, but the ventral masseteric ridge is carried forward as a heavy shelf to a point just behind the mental foramen. The ventral ridge is extremely robust, while the dorsal ridge is strong but less elevated. The latter meets the ventral ridge under the anterior end of $P_4$. The mental foramen is situated just below the dorsal border of the anterior end of the mandible and closer to $P_4$ than the incisor. The diastema is short and the diastemal depression shallow.

The incisor is slender with a rounded anterior face. The enamel overlaps onto about one-fifth of the medial surface and one-third of the lateral surface.

In CM 9230, $P_4$ is quadricuspate, while in CNHM PM 8627 the premolar has only three cusps. In the latter specimen the metaconid, hypoconid, and entoconid are of equal size and height with a narrow, deep valley separating the metaconid and entoconid and a broader and equally deep valley separating the hypoconid and entoconid. The antero-external quarter of this tooth consists of a flat shelf with no indi-

cation of even a minute protoconid in this area. Between the hypoconid and entoconid at the posterior margin of the tooth there is a faint indication of a hypoconulid. In CM 9230 the three high spike-like cusps are present and there is also a well developed protoconid which rises almost to the same level as the metaconid. These two cusps are set close together, much more so than are the hypoconid and entoconid, but are separated by a deep valley. In this specimen the hypoconulid is somewhat larger than in CNHM PM 8627.

The first lower molars are identical in the two specimens. There are two transverse rows of three cusps each, completely separated by a deep central valley. As in the upper molars the teeth are cuspate rather than lophate. The protostylid and hypostylid are almost the same size as the four principal cusps. The anterior cingulum is elevated into a rather high, thin ridge and there is a deep valley between it and the protoconid and metaconid; it is fused with the protostylid about midway down the anterior face of that cusp. A posterior cingulum is present but it is narrow and low.

MEASUREMENTS IN MILLIMETERS

|  |  | CM 9006 | CM 10101 |
|---|---|---|---|
| Alveolar length | $P^4$-$M^3$ | 3.4 | 3.3 |
| $P^4$ | a-p | .9 | .7 |
|  | tr. | .5- .8 | .4- .8 |
| $M^1$ | a-p | .9 | .9 |
|  | tr. | 1.0- .9 | 1.0-1.0 |
| $M^2$ | a-p | .8 | — |
|  | tr. | .9- .9 | — |
| $M^3$ | a-p | .6 | — |
|  | tr. | .7 | — |

MEASUREMENTS IN MILLIMETERS

|  |  | CM 9230 | CNHM PM 8627 |
|---|---|---|---|
| Alveolar length | $P_4$-$M_3$ | — | 3.4 |
| Length of diastema |  | 2.4 | — |
| Depth below $M_1$ |  | 2.7 | 2.7 |
| $P_4$ | a-p | .6 | .6 |
|  | tr. | .4- .6 | .4- .6 |
| $M_1$ | a-p | .9 | .8 |
|  | tr. | .9 | .8 |
| $I_1$ | a-p | 1.1 | — |
|  | tr. | .4 | — |

AFFINITIES: In size these specimens appear to be slightly larger than the mean for the Orellan populations from northeastern Colorado discussed by Galbreath (1953: 65). However, a larger sample from Pipestone would certainly give a greater size range than is at present exhibited, and the difference is so small between the two Colorado populations and that from Pipestone that it does not in itself warrant specific recognition of the Montana material. Also, the structure of the cheek teeth and the variation seen in this sample coincide well with that observed in the later Colorado populations.

It is somewhat surprising that the morphological variation observed in the middle Oligocene populations is duplicated in the early Oligocene Pipestone material. Wood (1939: 560), Wilson (1949: 115), and Galbreath (1953: 65) have all suggested that the four-cusped condition of $P_4$ was primitive and that the three-cusped condition represented reduction from that more primitive stage. This would certainly seem the most probable evolutionary pattern in *Heliscomys*. However, if this were the case, it would appear that the reduction and eventual loss of the protoconid on $P_4$ was not under strong selective pressure since both the three-cusped and four-cusped condition persisted at least from the early Oligocene through the middle Oligocene and possibly even somewhat later. This variation suggests that *Heliscomys* was ancestral to *Proheteromys*. Fragmentation and isolation of portions of an *Heliscomys vetus* population such as is represented at Pipestone Springs or in northeastern Colorado could have resulted in the evolution of one line which lost the premolar protoconid entirely and another which emphasized the enlargement of $P_4$, retention of the protoconid, and eventual addition of a fifth cusp, the anteroconid. The first line could have led to *H. woodi,* known from the early Miocene, and the second line to *Proheteromys*.

Recently Reeder (1960) has described two genera of heteromyids from the middle Oligocene. One, *Apletotomeus,* has a four-cusped $P_4$ with a slight swelling anterior to the metaconid; the other, *Akmaiomys,* has a rather large anteroconid which is antero-posteriorly elongated. *Apletotomeus crassus* could easily be derived from *Heliscomys vetus* and it is quite probable that the two species are congeneric. The large size of the incisor would appear to separate these populations as distinct species but this character alone does not warrant a generic distinction between the two. *Akmaiomys incohatus* resembles *Proheteromys floridanus* in the pattern of $P_4$ and certainly seems referable to that genus. The antero-posterior elongation of the anteroconid on $P_4$ is vari-

able in *P. floridanus* (Black, 1963a), some specimens showing a greater elongation of the anteroconid than is seen in *Akmaiomys crassus;* while in other specimens the anteroconid is minute to absent. Galbreath (1953: 66) originally referred the type of *Akmaiomys crassus* to *Proheteromys?* sp. This assignment seems likely, especially in view of the variation now known for $P_4$ of *Proheteromys floridanus.*

The variation seen in $P_4$ of both *Heliscomys* and *Proheteromys* has led to considerable confusion as regards the proper specific and generic determination of Oligocene and early Miocene specimens of heteromyids. It is quite possible that species assigned to *Heliscomys, Proheteromys, Mookomys, Apletotomeus,* and *Akmaiomys* are all congeneric and that we are dealing with a highly variable set of populations none of which have yet reached the perognathine-heteromyine level of development; this was first suggested by Wilson (1960: 75). Only a thorough review of the Oligocene *Heliscomys* populations can hope to solve these problems.

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